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ON DOMINANCE RELATIONS AND THE STRUCTURE OF ANIMAL SOCIETIES: II. SOME EFFECTS OF POSSIBLE SOCIAL FACTORS—*H. G. Landau* - - - - - - - - - - - - - - - 245

DETERMINATION OF THE SENSITIVE VOLUME BY IRRADIATION AND THE IONIZATION DENSITY—*I. Opatowski* - - - - - - 263

DIFFUSION AND RECOMBINATION OF PRODUCTS OF IONIZING RADIATIONS—*I. Opatowski and F. R. Tangherlini* - - - 273

MATHEMATICAL BIOSOCIOLOGY OF BELIEFS AND PREJUDICES—*N. Rashevsky* - - - - - - - - - - - - - - 289

THE KINETICS OF INVERTASE ACTION—*R. L. Plunkett and C. L. Gemmill* - - - - - - - - - - - - - - 303

THE GAME OF "GOSSIP" ANALYZED BY THE THEORY OF INFORMATION—*Edgar Reich* - - - - - - - - - - - 313

A NOTE ON THE PROBLEM OF CYCLES IN RANDOM NETS—*A. Shimbel* - - - - - - - - - - - - - - - - 319

A NEUROBIOPHYSICAL INTERPRETATION OF CERTAIN ASPECTS OF THE PROBLEM OF RISKS—*H. D. Landahl* - - - - - - 323

BOOK REVIEW—JAMES T. CULBERTSON, Consciousness and Behavior: A Neural Analysis of Behavior and Consciousness—*Anatol Rapoport* - - - - - - - - - - - - - - 337

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BULLETIN OF
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ON DOMINANCE RELATIONS AND THE STRUCTURE OF ANIMAL SOCIETIES: II.

SOME EFFECTS OF POSSIBLE SOCIAL FACTORS

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In a previous paper (Landau, 1951) it was shown that a society with a dominance relation would rarely tend to be close to the hierarchy in structure if dominance is determined solely by the inherent characteristics of the members. Here we consider the effects of other factors, due to social rank or to the outcome of previous encounters which affected dominance.

The following results are obtained. A uniform bias against reversal of dominance will have no effect on the stationary distribution of the structure of the society. If the probability of dominance is a linear function of the previously established score (number of members dominated), there will be a small tendency for the society to move toward the hierarchy; but this is negligible for large societies. If a member never challenges another whose score exceeds his own by two or more, or if he can never dominate if he should challenge, then the hierarchy is the only stable structure.

From the last result it is concluded that social factors which restrict challenges or the probability of dominance could easily account for societies close to the hierarchy, such as are observed in flocks of domestic hens.

The effectiveness of social bias in establishing hierarchies is much greater in small societies than in large ones.

1. INTRODUCTION. This paper continues the study of the structure of societies with a dominance relation between every pair of members. Familiarity with the previous paper (Landau, 1951, referred to as I) is assumed.

One of the principal conclusions of I was that if dominance is determined solely by the inherent characteristics of the members, then a society with a dominance relation would rarely be close to the hierarchy. By inherent characteristics we mean all those which are not affected by the social status, i.e., the dominance relations, of any of the members or by the results of any previous encounters in which dominance relations were affected. Since, however, societies which are hierarchical in structure, except perhaps for a small number of triangles* $(j \succ k, k \succ l, l \succ j)$ are known to occur, particularly

*A list of symbols is given on page 261.

among domestic hens, it is important to consider whether social factors could produce hierarchies. By social factors we mean all those factors affecting dominance which are not due to inherent characteristics of the members; i.e., social factors are those due to the existing or previous social structure, or dominance relations, or to the outcome of any previous encounters affecting dominance.

This paper considers the mathematical aspects of some possible social factors. Certain assumptions are made as to the operation of factors which depend on the previous history of the society and its members, and conclusions as to the effect on the structure of the society are derived. A detailed discussion of the mechanism of such factors in social, psychological or physiological terms is not attempted. Thus, whether a particular factor could be ascribed to social lag, conditioning or hormone concentration will not be discussed.

The essential difference between the present considerations and those of I is as follows. In I, the picture was that of the n members of the society coming together and engaging in $N = n(n-1)/2$ contests—one for each pair, or a single round robin—with the result of each contest fixing the direction of dominance for the pair involved. The outcome of each contest was completely *independent* of that of any other contest, but depended only on inherent characteristics of the members. Our present picture is that the N dominance relations have been determined by some process, and that thereafter contests (or encounters) occur between some of the pairs. Only one contest is supposed to occur at a time; and we consider various assumptions about the way in which the probabilities of contests or of their outcomes may depend on the previous dominance relations. Each such contest may change the structure of the society, and we wish to be able to draw conclusions about the way in which the structure will vary.* Considerations of this kind were introduced by A. Rapoport (1949, 1950), who calculated some effects of social factors in societies with three members.

A change of structure can occur, as a result of the contests we are considering, only if the dominance relation is reversed, but reversal of a dominance relation does not necessarily result in a different structure. This point will, of course, be considered in detail in

*Other possible treatments might be to consider the development of the structure from an initial state when no dominance relations had yet been established, through the successive stages when $1, 2, \cdots, N$ dominance relations have been established. Or again, we might consider what happens when a new member is introduced into a society with an established structure, and thus build up our society by successively adding new members. These approaches will not be treated here.

connection with the different factors which are assumed. The kinds of factors to be considered here include bias against reversal of dominance, the probability of dominance being dependent on previous score, and the probability of the subordinate member of a pair challenging the dominant one being dependent on previous score.

In I, we considered the society to be a random sample of n individuals from a population with a given distribution of inherent characteristics. Here we do not consider the society to be a random sample, but are instead looking at a society of n fixed individuals and wish to determine how the social structure changes with time. In some cases it is also assumed that the individuals are the same with respect to inherent characteristics.

We are interested in determining whether the effect of social factors is to lead to an ultimate stable structure for the society, and, if so, what kind of structure. In general there is no single stable structure, and we would like to be able to characterize the distribution of structures through which the society passes as contests go on.

2. MATHEMATICAL METHOD. The effect of social factors cannot be treated by the mathematical technique used in I, because the probability of dominance now depends on existing dominance relations. The mathematical procedure for handling problems of this kind is the theory of Markov chains. An excellent introduction to this theory is given in W. Feller (1950), and a more detailed account can be found in M. Fréchet (1938). For terminology and results not proven here we refer to Feller.

The theory of Markov chains* is concerned with a system which can exist in several states, $E_1, E_2, E_3, \cdots$. If the system is in state E_α, the probability that it will change to state E_β is given by the transition probability $a_{\alpha\beta}$.

In the application to societies with dominance relations, the states E_α are the possible structures of the society. The transition probabilities $a_{\alpha\beta}$ then give the probability that the structure will change from E_α to E_β as the result of an encounter.

In applying the Markov chain theory we are faced by the difficulty that the measure of structure which was used in I, the hierarchy index h, cannot be used to define the E_α. This is because, as was pointed out in I, more than one dominance structure can have the same score structure and hence the same value of h, but the determination of the transition probabilities will, in general, require the

*Only finite chains are needed here, and it is assumed that the transition probabilities are constant.

knowledge of dominance structure. Thus in the example given in I (p. 3), if in the first matrix the dominance relation $5 \succ 1$ is reversed to $1 \succ 5$, we obtain a structure with $V = (4,2,2,2,0)$, but this score structure cannot be obtained from the second matrix by any single reversal of a dominance relation.

The fact that h alone does not suffice for the treatment of social factors means that our considerations in the following are more involved than in I. However, h is still a useful measure as will be seen below.

First we wish to show that under certain conditions a stationary distribution of structures independent of the initial structure will exist. A simple sufficient (but not necessary) condition is that all $e_{jk}p_{jk} > 0$, where e_{jk} is the probability of an encounter between members j and k, and p_{jk} is the probability that $j \succ k$ after the encounter. This condition implies that in any structure the probability that any dominance relation be either reversed or maintained is not zero. We can now refer to Feller (1950; Theorem 2, p. 325). The non-zero probability of maintaining any dominance relation means that $a_{\alpha\alpha} > 0$, hence the chain is aperiodic. Also since any reversal of dominance relations has a non-zero probability, it is possible to go from any structure to any other by a finite number of one-step transitions, so that the chain is irreducible. From the theorem referred to, it then follows that there is a stationary probability distribution, u_α, probability of the structure E_α, satisfying

$$u_\alpha \geq 0, \sum_\alpha u_\alpha = 1, \tag{1}$$

and

$$u_\alpha = \sum_\beta u_\beta a_{\beta\alpha}. \tag{2}$$

This theorem was proven by Rapoport (1949) without referring to Markov chains.

The interpretation of this stationary distribution of structures is as follows. As encounters occur which may change dominance relations, the structure of the society changes going from E_{α_1} to E_{α_2}, E_{α_3}, etc. The distribution u_α then gives the distribution of the structures which the society takes on during the course of time. If we assume that encounters occur at equal intervals of time (since we are not concerned here with the actual time rate of encounters), then u_α gives the fraction of the time during which the society has the structure E_α.

This conclusion can be related to the work in I. In I we considered societies of n individuals drawn from a population with a given distribution of inherent characteristics which determined dominance probability. These individuals engaged in a single round robin. The resulting distribution of structures depended on two sets of random factors: (1) the inherent characteristics of the particular n individuals, and (2) the outcome of the contests. We now omit the first set of random factors, i.e., we now consider a society of n fixed individuals with inherent characteristics determining dominance probability; then the distribution due to the varying possible outcome of the contests is exactly the same as would be given by the distribution u_a above, by using the Markov chain theory. This is to be expected from the uniqueness of the stationary distribution for finite, aperiodic irreducible chains (Feller, 1950, p. 329), and an explicit proof is given in the Appendix (Theorem A1). This property is referred to as the ergodic property of such chains. To restate: If dominance is affected only by inherent characteristics then a society whose structure changes due to continued encounters will in the course of time pass through the same distribution of structures as would result from the possible outcomes of round robin tournaments for that society.

In this connection, it is worth stating the formula for $E(h)$ for a society of n fixed individuals with inherent characteristics determining dominance probability. This was not explicitly stated in I, but follows directly from (7) and (15) there, which give

$$E(h) = \frac{3}{n+1}\left[1 + \frac{1}{n(n-1)} \sum_{\substack{i,j,k \\ j \neq k}} g_{ij} g_{ik}\right]. \tag{3}$$

3. Bias Against Reversal of Dominance. The first social factor which we consider is that of bias against reversal of dominance. This could be interpreted as some sort of conservative factor or tendency to maintain existing dominance relations.

We consider a society of n individuals with inherent characteristics which give the dominance probabilities $p_{jk}(0)$, the probability that $j > k$, before any encounters have occurred. We now assume that if actually $j > k$, then the probability of reversal of dominance at the next encounter is

$$p_{kj} = (1 - \varepsilon) p_{kj}(0), \tag{4}$$

with

$$0 \leq \varepsilon < 1 .$$

This says that dominance once having been established, the probability of reversal is reduced compared to the original probability of the reversed direction of dominance. We are also making here the very restrictive assumption that the factor $1 - \varepsilon$, by which the probability of reversal is reduced, is the same for all pairs, i.e., the bias is uniform.

It is shown in the Appendix (Theorem A2) that under these assumptions the stationary distribution, u_a, is independent of the bias against reversal of dominance, ε.

This result is a little surprising, especially when we notice that the excluded case, $\varepsilon = 1$, means that no reversal is possible so that the structure can never change. But Theorem A2 states that any uniform bias, no matter how large as long as it permits a non-zero probability of reversals, has no effect on the ultimate distribution of structures. Of course, a large ε means that the structure is less likely to change. It is more likely to remain as it is than shift to a new structure,* but as long as $\varepsilon < 1$ there is a positive probability of shifting, and once shifted it again tends to remain in the new structure. However, in the long run the fraction of time spent in each structure is the same as if there were no bias against reversal.

Of course, the assumption that the bias against reversal of dominance is uniform is much more special than we would like. Any socially conservative factors that operated against reversal of dominance would probably also depend on other factors, such as the relative social rank of the pair of individuals concerned. However, it has not as yet been possible to carry through the treatment of bias against reversal on more general assumptions except for the case treated in Section 5. For very small societies the complete calculations can be made in detail, and this has been done by Rapoport (1950) for $n = 3$.

4. Dominance Probability a Linear Function of Score Difference. Another possibility for the manner in which a social or psychological factor might operate is through affecting the dominance probability according to the scores of the individuals. The score of an individual is, of course, a measure of his social rank.

In the case of a flock of hens it is not reasonable to assume that each hen counts the number of hens pecked by each of her flock-mates, compares this with her own score, and acts accordingly. However, she can be expected to observe roughly relatively how often a particu-

*The tendency to persist in one state could be measured by the serial correlation coefficient of h. This would increase with increasing ε.

lar hen pecks or is pecked, and that her behavior will be influenced by this rough estimate of social rank. This seems to be especially true of the behavior toward those hens who are near the top and also those near the bottom.

As a first case, let us assume that the probability of dominance at any time is a linear function of the score difference of the pair involved, i.e., we take as the probability that $j > k$ at time t to be given by

$$p_{jk} = \tfrac{1}{2}\,[1 + \omega(v_j - v_k)], \tag{5}$$

where ω is a constant and v_j is the score from the preceding encounters. The dominance probability is here assumed to depend only on score difference and not on any other factors, either inherent or social. We also assume that the probability of encounter is the same for all pairs.

On this basis, the expected value of the hierarchy index, $E(h)$, can be calculated. Here, since the structure of the society changes with time, $E(h)$ is the average value of h over a long period. It is shown in the Appendix that

$$E(h) = \frac{H}{1 - \omega(n-2)/2}, \tag{6}$$

where $H = 3/(n+1)$ is $E(h)$ for $\omega = 0$. The case $\omega = 0$ is that of no dominance bias, and the present formula, of course, gives the same result as found in I, equation (49).

In interpreting (6) it must be remembered that p_{jk} in (5) is a probability, so $p_{jk} \leq 1$; and since $v_j - v_k$ can be as large as $n - 1$, we must have

$$\omega \leq \frac{1}{n-1}. \tag{7}$$

We also assume $\omega \geq 0$. For negative ω see Section 6.

For small n, when ω has the maximum value given by (7), the structure of the society will be close to the hierarchy: for $n = 3$, $E(h) = 1$ and for $n = 5$, $E(h) = 4/5$. But for large n, we have

$$E(h) \cong 6/n, \tag{8}$$

so that the society will be near equality more of the time than it is near the hierarchy.

It is not hard to see the reason for this result for large n. The limitation $\omega \leq 1/(n-1)$, made necessary by the assumption of lin-

earity, means that for large n, the bias in favor of the higher ranking member of any pair will not be appreciable until the difference in score becomes relatively large. As n increases, the proportion of pairs for which the score difference is large will decrease, so that the effect of the linear bias decreases.

5. BIASES WHICH MAKE THE HIERARCHY CERTAIN. It was suggested by Rapoport (1950) that if encounters and reversals are confined to individuals of equal social rank, then the hierarchy would result. This would be a very severe restriction, and what we now show is that the hierarchy is the only stable structure under rather less severe restrictions on possible encounters and reversals of dominance. Theorem A4 of the Appendix states that if the probability that $j \succ k$ is equal to 1 whenever $v_j \geq v_k + 2$, then the hierarchy is the only stable structure. This restriction is equivalent to saying that reversal of dominance is impossible if the subordinate member's score is less than that of the dominant member of the pair by two or more. Still another statement of the same result would be that the structure is certain to become the hierarchy, if a member never challenges another whose score exceeds his own by two or more.

For $n = 3$, the present extreme bias is the same as the maximum linear bias, so that we have another way of seeing why the hierarchy is the only stable state in this case.

It should be noted that the hierarchy we are considering here is not stable in the sense of the individual members maintaining their relative positions. Instead, it would be quite possible for individuals

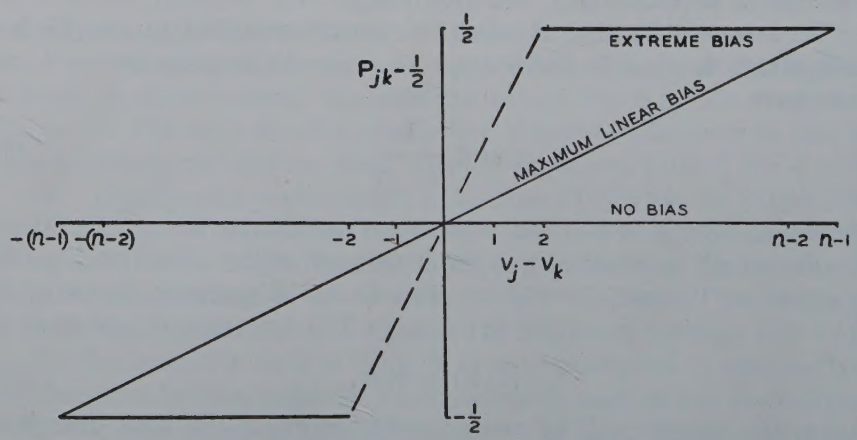

FIGURE 1. The relation between the biases which increase dominance probability according to score difference. Note that for the extreme bias, p_{jk} is unspecified for $|v_j - v_k| \leq 1$.

in adjacent ranks to be constantly interchanging positions; but these are the only interchanges which would be possible and they do not alter the hierarchical structure. The zoologist studying a flock of hens would probably want to define stability in terms of the position of the individual hens remaining unchanged. Our result does not refer to stability in this sense, but it can be pointed out that if in the above theorem we replace the score difference of two by one, we get this kind of stability. This means that reversals can occur only between individuals with the same score. Once the hierarchy is attained, there could be no further change of dominance relations.

6. General Remarks. We have been looking for social biases that would give near-hierarchical structures. Figure 1 illustrates the cases treated of a bias that depends on score difference. For no bias, that is, $p_{jk} - \frac{1}{2} = 0$, and even for the maximum linear bias, the hierarchy will be rare except in very small societies. The extreme bias just treated does make the hierarchy a certainty, but is probably too restrictive to be realistic. It would seem likely that biases lying between the linear one and the extreme would make the hierarchy more likely, even for large n as the bias approached the extreme case. It has not yet been possible to carry out the analysis of the effect of such biases.

However, we can conclude that a social bias which makes the preservation of dominance more likely the greater the difference in social rank (as measured by score difference) could account for the prevalence of near-hierarchical structures in flocks of hens. Also, the larger the society the stronger does the bias need to be to establish the hierarchy; or, in other words, equal biases will be less effective in making for the hierarchy in a large compared to a small society. This statement is, of course, not exact because we have given no measure of the strength of a social bias. It does agree with the observed fact that very large hen flocks are less likely to have the hierarchical structure.

So far we have mainly been trying to account for the hierarchy, and have implicitly assumed that all biases were in this direction. It seemed, at first, unreasonable to consider negative values of ε or ω or reversal of the inequality in the last section. However, it occurs to the writer that this may be a bias in his own thinking induced by the culture pattern of his own society. For example, R. Benedict (1934) describes the socially enforced habit of cooperation among the Zuñi. Perhaps biases favoring the subordinate member should be given equal consideration, if only to indicate what might occur in

a cooperative society. There is no difference in the mathematics, only changes of sign are needed.

Thus in Section 3, the uniform bias ε could be negative [so long as $(1-\varepsilon)p_{kj}(0) \leq 1$] and then favor reversal of dominance. As before, this would have no effect on the stationary distribution, but now instead of tending to persist in its existing structure the society would tend to shift away from the existing structure.

Making ω negative would tend to move any society, even small ones, toward equality. For $\omega = -1/(n-1)$ (its largest negative value), $E(h) \cong 2/n$ for large n.

Reversing the inequality in Section 5 can be easily seen to result in h having its lowest possible value; i.e., zero for n odd or $3/(n^2-1)$ for n even. The only possible structures are the equality, or a structure as close to it as possible for n even.

APPENDIX

The dominance structure was defined in I as a set of matrices such that any two matrices of the set could be transformed into each other by a permutation of rows and corresponding columns. For the application of Markov chain theory it is more convenient to take as the individual states not the dominance structure but the individual matrices used to define it, i.e., each state is a skew-symmetric matrix, M_α with the elements $m_{\alpha,jk}$ such that

$$m_{\alpha,jk} = 1 \text{ if } j \succ k.$$

Taking these matrices to be our states amounts to considering two states as distinct when different individuals occupy corresponding positions in the two, even though one matrix can be transformed into the other by a row and column permutation; i.e., renaming the individuals. The states thus defined form a finite Markov chain with constant transition probabilities, and the resulting stationary distributions can be stated in terms of the distribution of dominance structures by combining the probabilities, u_α, for those states which belong to the same dominance structure.

The advantage of using these matrices for the states is immediately apparent. Any reversal of a dominance relation will now carry the state M_α into a different state. There will be exactly N such states, which we will denote by $\mathrm{M}_{\alpha'}$. Thus the transition probabilities $a_{\alpha\beta}$ (and $a_{\beta\alpha}$) are in every case equal to zero except for $\beta = \alpha$ or one of the N values of α'. Also each such transition, $\mathrm{M}_\alpha \to \mathrm{M}_{\alpha'}$ or $\mathrm{M}_{\alpha'} \to \mathrm{M}_\alpha$, is associated with the reversal of dominance between a particular pair of individuals, which we denote by $j_{\alpha'}$ and $k_{\alpha'}$.

The total number of states is 2^N.

The theorem of Section 2 can now be proven as follows.

Theorem A1. If the dominance probabilities, p_{jk}, depend only on inherent characteristics, and all encounters are equally probable, then the directly calculated distribution of structures is the same as the stationary distribution.

Proof: Let $u_\alpha^{(0)}$ be the probability of M_α in the initial distribution which is the same as that directly calculated in I, and $u_\alpha^{(n)}$ be the distribution after n encounters. We show that $u_\alpha^{(0)} = u_\alpha^{(1)}$; hence $u_\alpha^{(0)} = u_\alpha^{(n)}$ for all n. Since the stationary distribution is $u_\alpha = \lim_{n\to\infty} u_\alpha^{(n)}$, it follows that $u_\alpha = u_\alpha^{(0)}$.

Now

$$u_\alpha^{(0)} = \prod_{j<k} P(m_{\alpha,jk}), \tag{9}$$

where

$$\begin{aligned} P(m_{\alpha,jk}) &= p_{jk}, \text{ if } m_{\alpha,jk} = +1, \\ &= p_{kj} = 1 - p_{jk}, \text{ if } m_{\alpha,jk} = -1. \end{aligned}$$

If the one-step transition $M_{\alpha'} \to M_\alpha$ is possible, then $u_{\alpha'}^{(0)}$ differs from $u_\alpha^{(0)}$ in a single term in (9), namely,

$$P(m_{\alpha',j_{\alpha'}k_{\alpha'}}) = 1 - P(m_{\alpha,j_{\alpha'}k_{\alpha'}}),$$

which replaces

$$P(m_{\alpha,j_{\alpha'}k_{\alpha'}}),$$

so that

$$u_{\alpha'}^{(0)} = u_\alpha^{(0)} \frac{1 - P(m_{\alpha,j_{\alpha'}k_{\alpha'}})}{P(m_{\alpha,j_{\alpha'}k_{\alpha'}})}. \tag{10}$$

The denominator cannot be zero, since this would imply $a_{\alpha'\alpha} = 0$.

We have

$$a_{\alpha'\alpha} = \frac{1}{N} P(m_{\alpha,j_{\alpha'}k_{\alpha'}}), \tag{11}$$

where $1/N$ is the probability of encounter. Also

$$a_{\alpha\alpha} = \frac{1}{N} \sum_{j<k} P(m_{\alpha,jk}). \tag{12}$$

Now

$$u_\alpha^{(1)} = \sum_{\beta=1}^{2^N} u_\beta^{(0)} a_{\beta\alpha}.$$

Using (10), (11), (12) we obtain

$$
\begin{aligned}
u_a^{(1)} &= \frac{u_a^{(0)}}{N} \sum_{j<k} P(m_{a,jk}) + \frac{u_a^{(0)}}{N} \sum_{a'=1}^{N} [1 - P(m_{a,j_{a'}k_{a'}})] \\
&= \frac{u_a^{(0)}}{N} \sum_{j<k} P(m_{a,jk}) + \frac{u_a^{(0)}}{N} \sum_{j<k} [1 - P(m_{a,jk})] \\
&= u_a^{(0)},
\end{aligned}
$$

so that the initial distribution is unchanged, and by the remarks above it must be the same as the stationary distribution.

From now on we use the convention that the pair $j_{a'}, k_{a'}$ are related as follows:

$$
\begin{aligned}
&j_{a'} \succ k_{a'} \text{ in } \mathrm{M}_a, \text{ or } m_{a,j_{a'}k_{a'}} = +1; \\
&k_{a'} \succ j_{a'} \text{ in } \mathrm{M}_{a'}, \text{ or } m_{a',j_{a'}k_{a'}} = -1.
\end{aligned} \tag{13}
$$

We now prove the theorem of Section 3.

Theorem A2. The stationary distribution is independent of uniform bias against reversal, ε.

Proof: The transition probabilities are

$$
\begin{aligned}
&a_{aa'} = e_{j_{a'}k_{a'}} p_{k_{a'}j_{a'}}, \\
&a_{a\beta} = 0, \text{ for } \beta \neq a, a', \\
&a_{aa} = 1 - \sum_{\substack{\beta=1 \\ \beta \neq a}}^{2^N} a_{a\beta}.
\end{aligned} \tag{14}
$$

We indicate the dependence of the probabilities on ε by writing $a_{a\beta}(\varepsilon)$, etc. Then, since the probability of any reversal is

$$
p_{kj}(\varepsilon) = (1 - \varepsilon) p_{kj}(0), \tag{15}
$$

we have

$$
a_{a\beta}(\varepsilon) = (1 - \varepsilon) a_{a\beta}(0), \text{ for } \beta \neq a.
$$

Since we assume that a stationary distribution exists,

$$
\begin{aligned}
&u_a(\varepsilon) = \sum_{\beta=1}^{2^N} u_\beta(\varepsilon) a_{\beta a}(\varepsilon), \\
&\sum_{a=1}^{2^N} u_a = 1.
\end{aligned} \tag{16}
$$

Using (14) and (15)

$$u_\alpha(\varepsilon) = u_\alpha(\varepsilon)\,[1 - (1-\varepsilon) \sum_{\beta\neq\alpha} a_{\alpha\beta}(0)]$$
$$+ (1-\varepsilon) \sum_{\beta\neq\alpha} u_\beta(\varepsilon)\, a_{\beta\alpha}(0)\,.$$

Since $1 - \varepsilon > 0$, this gives

$$0 = -u_\alpha(\varepsilon) \sum_{\beta\neq\alpha} a_{\alpha\beta}(0) + \sum_{\beta\neq\alpha} u_\beta(\varepsilon)\, a_{\beta\alpha}(0)$$
$$= -u_\alpha(\varepsilon)\,[1 - a_{\alpha\alpha}(0)] + \sum_{\beta\neq\alpha} u_\beta(\varepsilon)\, a_{\beta\alpha}(0)\,,$$

or

$$u_\alpha(\varepsilon) = \sum_{\beta=1}^{2^N} u_\beta(\varepsilon)\, a_{\beta\alpha}(0)\,,$$

but these are the equations satisfied by $u_\alpha(0)$. Hence from the uniqueness of the solution of (16) it follows that u_α is independent of ε.

From this proof we get a result about Markov chains in general. If the transition probabilities, $a_{\alpha\beta}$ for $\alpha \neq \beta$, are each multiplied by a constant λ, $0 < \lambda \leq 1$, and to each $a_{\alpha\alpha}$ is added $(1 - \lambda)\,(1 - a_{\alpha\alpha})$, then the stationary distribution remains unchanged.

We now derive Equation (6).

Theorem A3. If

$$p_{jk} = \tfrac{1}{2}\,[1 + \omega(v_j - v_k)]$$

where ω is a constant, and

$$e_{jk} = 1/N \text{ for all } j \text{ and } k\,, \tag{17}$$

then

$$E(h) = \frac{H}{1 - \omega(n-1)/2}.$$

Proof: Consider first the unbiased case, $\omega = 0$, $p_{jk} = 1/2$, and denote the transition probabilities in this case by $c_{\alpha\beta}$, so that

$$\begin{aligned} &c_{\alpha\alpha'} = 1/2N \text{ for the } N \text{ values of } \alpha', \\ &c_{\alpha\beta} = 0 \quad \text{for} \quad \beta \neq \alpha\,, \alpha', \\ &c_{\alpha\alpha} = 1/2\,. \end{aligned} \tag{18}$$

We also note that $c_{\alpha\beta} = c_{\beta\alpha}$, or the transition probability matrix is symmetric.

Let h_a be the hierarchy index for M_a and $M = 12/(n^3 - n)$ so $h = M \sum_{j=1}^{N} (v_j - v)^2$. Then the change in h due to the transition $M_a \to M_a'$ is

$$\begin{aligned} h_{a'} - h_a &= M\,[(v_{j_{a'}} - 1 - \bar{v})^2 + (v_{k_{a'}} + 1 - \bar{v})^2 \\ &\quad - (v_{j_{a'}} - \bar{v})^2 - (v_{k_{a'}} - \bar{v})^2] \\ &= 2M(v_{k_{a'}} - v_{j_{a'}} + 1)\,. \end{aligned} \tag{19}$$

We need to evaluate the sums:

$$\begin{aligned} S_1(a) &= \sum_{\beta=1}^{2^N} c_{a\beta}\, h_\beta, \\ S_2(a) &= \sum_{\beta=1}^{2^N} c_{a\beta}\, h^2{}_\beta. \end{aligned} \tag{20}$$

Using (18)

$$S_1(a) = \frac{1}{2} h_a + \frac{1}{2N} \sum_{a'=1}^{N} h_{a'};$$

then, from (19),

$$S_1(a) = h_a + M - \frac{M}{N} \sum_{a'=1}^{N} \left(v_{j_{a'}} - v_{k_{a'}} \right). \tag{21}$$

The last summation is the sum of the score differences, $v_j - v_k$, in M_a over all pairs with $j > k$, i.e., $\sum_{j>k} (v_j - v_k)$. In this sum, each v_j occurs v_j times with a positive sign (once for each member dominated by j) and $(n - 1 - v_j)$ times with a negative sign (once for each member who dominates j), so that

$$\begin{aligned} \sum_{j>k} (v_j - v_k) &= \sum_{j=1}^{n} \left[v_j{}^2 - (n - 1 - v_j)\, v_j \right] \\ &= 2 \sum_{j=1}^{n} v_j \left(v_j - \frac{n-1}{2} \right) = \frac{2}{M} h_a. \end{aligned} \tag{22}$$

Hence

$$S_1(a) = M + \left(1 - \frac{2}{N} \right) h_a; \tag{23}$$

$S_2(\alpha)$ is similarly evaluated. It involves

$$\sum_{j>k} (v_j - v_k)^2 = \frac{1}{2} \sum_{j=1}^{n} \sum_{k=1}^{n} (v_j - v_k)^2$$

$$= \frac{1}{2} \sum_{j=1}^{n} \sum_{k=1}^{n} [(v_j - \bar{v})^2 + (v_k - \bar{v})^2] \tag{24}$$

$$= n \sum_{j=1}^{n} (v_j - \bar{v})^2 - \left[\sum_{j=1}^{n} (v_j - \bar{v}) \right]^2 = \frac{n}{M} h_\alpha,$$

so that we obtain

$$S_2(\alpha) = 2M^2 + 2M\left(1 + \frac{n-4}{N}\right) h_\alpha + \left(1 - \frac{4}{N}\right) h^2{}_\alpha. \tag{25}$$

We can now write the transition probabilities for the general case, $\omega \neq 0$. Using (5), (18), and (19) we get for $\alpha \neq \beta$,

$$a_{\alpha\beta} = c_{\alpha\beta}\left[1 - \omega - \frac{\omega}{2M}(h_\alpha - h_\beta)\right], \tag{26}$$

and, using $\sum_{\beta=1}^{2^N} a_{\alpha\beta} = 1$ and $S_1(\alpha)$, we get

$$a_{\alpha\alpha} = \frac{1}{2}\left[1 + \frac{\omega}{H} h_\alpha\right], \tag{27}$$

where $H = \dfrac{3}{n+1}$.

Now if u_α is the stationary distribution then

$$u_\alpha = \sum_{\beta=1}^{2^N} u_\beta a_{\beta\alpha} = \sum_{\beta} u_\beta c_{\beta\alpha}\left[1 - \omega - \frac{\omega}{2M}(h_\beta - h_\alpha)\right] + u_\alpha \frac{\omega}{2}\left(1 + \frac{h_\alpha}{H}\right). \tag{28}$$

Also

$$
\begin{aligned}
E(h) &= \sum_{\alpha=1}^{2^N} h_\alpha u_\alpha \\
&= \sum_\alpha \sum_\beta h_\alpha u_\beta c_{\beta\alpha} \left[1 - \omega - \frac{\omega}{2M} (h_\beta - h_\alpha) \right] \\
&+ \frac{\omega}{2} \sum_\alpha h_\alpha u_\alpha \left(1 + \frac{h_\alpha}{H} \right) \\
&= \frac{\omega}{2} \left[E(h) + \frac{1}{H} E(h^2) \right] \\
&+ \sum_\beta u_\beta \sum_\alpha h_\alpha c_{\beta\alpha} \left[1 - \omega \left(1 + \frac{h_\beta}{2M} \right) + \frac{\omega}{2M} h_\alpha \right] .
\end{aligned}
\tag{29}
$$

Using $S_1(\alpha)$ and $S_2(\alpha)$, these sums can be evaluated. The term in $E(h^2)$ cancels out and we finally obtain

$$E(h) = \frac{H}{1 - \omega(n-1)/2}.$$

The theorem on biases which lead to the hierarchy is the following.

Theorem A4. If

$$p_{jk} = 1 \text{ for } v_j - v_k \geq 2 \tag{30}$$

and

$$e_{jk} p_{jk} > 0 \text{ for } v_j = v_k , \tag{31}$$

then the hierarchy is the only stable structure.

Proof: The proof depends on Equation (19) which shows that h can decrease by reversals, from $j_{\alpha'} \succ k_{\alpha'}$ to $k_{\alpha'} \succ j_{\alpha'}$, only when $v_{k_{\alpha'}} - v_{j_{\alpha'}} < -1$ before reversal; otherwise, h is either unchanged or increases.

Suppose that the structure is hierarchical. Then all the v's are different and if $j \succ k$ then $v_j > v_k$. From (30) a reversal of $j_{\alpha'} \succ k_{\alpha'}$ to $k_{\alpha'} \succ j_{\alpha'}$ is possible only for $v_{k_{\alpha'}} = v_{j_{\alpha'}} - 1$. However, such a reversal according to (19) leaves h unchanged. For the hierarchy $h = 1$, and this is the only dominance structure with this value of h. So that a matrix M_α corresponding to the hierarchy can change only into an $M_{\alpha'}$ which also corresponds to the hierarchy. The hierarchy is stable.

Now suppose the structure is not the hierarchy. Then h cannot decrease because as we have seen from (19) this would require $v_{k_{a'}} - v_{j_{a'}} < -1$, whereas (30) makes the probability of such a reversal equal to zero. Also since $e_{jk}p_{jk} > 0$, for $v_j = v_k$ reversals of dominance between individuals of equal score must occur. This means h cannot remain constant indefinitely, if the structure is not hierarchical. Any structure other than the hierarchy is unstable. Since h can take on only a finite number of values it must eventually reach and maintain the value $h = 1$. This completes the proof.

In the language of Markov chains, using dominance structures as our states, the hierarchy is an absorbing state and all other states are transient. It is also clear that this is the only bias depending on $v_j - v_k$ that leads to the hierarchy as the single stable state; for if $p_{jk} > 0$ for $v_j = v_k - 2$. then escape from the hierarchy is possible, and it is no longer an absorbing state.

LIST OF SYMBOLS

j, k, members of the society.
$j \succ k$, j dominates k.
n, number of members in the society.
$N = \dfrac{n(n-1)}{2}$.
E_a, the possible structures of the society.
$a_{a\beta}$, probability of transition from E_a to E_β.
$V = (v_1, v_2, \cdots, v_n)$, the score structure of the society.
v_j, j's score or number of members dominated by j.
u_a, probability of E_a in stationary distribution.
$h = M \sum_{j=1}^{n} (v_j - \bar{v})^2$, hierarchy index.
$M = 12/(n^3 - n)$.
$\bar{v} = (n-1)/2$, mean of v_j.
$E(h)$, expected value of h.
$g_{jk} = p_{jk} - p_{kj}$.
p_{jk}, probability that $j \succ k$.
e_{jk}, probability of an encounter of j and k.
ε, factor giving bias against reversal of dominance.
ω, factor giving effect of $v_j - v_k$ on p_{jk}.
$H = 3/(n+1)$.
$c_{a\beta}$, transition probability $a_{a\beta}$ when all $p_{jk} = 1/2$.
$\mathbf{M}_a$, structure matrices.
$m_{a,jk}$, the element in the jth row and kth column of $\mathbf{M}_a$.
h_a, h of E_a or $\mathbf{M}_a$.
$S_1(\alpha) = \sum_{\beta=1}^{2^N} c_{a\beta}\, h_\beta$.

$$S_2(\alpha) = \sum_{\beta=1}^{2^N} c_{\alpha\beta} h^2{}_\beta .$$

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LITERATURE

Benedict, Ruth. 1934. *Patterns of Culture.* New York: Penguin Books.

Feller, W. 1950. *An Introduction to Probability Theory and Its Applications.* New York: John Wiley.

Fréchet, M. 1938. *Méthode des fonctions arbitraire. Théorie des événements en chaîne dans le cas d'un nombre fini d'états possible.* Paris: Gauthier-Villars.

Landau, H. G. 1951. "On Dominance Relations and the Structure of Animal Societies: I. The Effect of Inherent Characteristics." *Bull. Math. Biophysics,* **13**, 1–19.

Rapoport, A. 1949. "Outline of a Probabilistic Approach to Animal Sociology: II." *Bull. Math. Biophysics,* **11**, 273–81.

——— 1950. "Outline of a Probabilistic Approach to Animal Sociology: III." *Ibid.,* **12**, 7–17.

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DETERMINATION OF THE SENSITIVE VOLUME BY IRRADIATION AND THE IONIZATION DENSITY

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Lea's formula for the determination of size of the sensitive volume is corrected and applied to experiments on inactivation of the tobacco mosaic virus using three different wave lengths of x-rays. The purely geometric concept of the sensitive volume is not sufficient for explaining the known dependence of the inactivation of this virus on wave length. The concept of transfer of energy around the ionizing particles is discussed in this connection in a manner similar to that suggested by Pollard and Forro for the inactivation of the T — 1 phage, and results similar to those given by these authors are obtained from an analysis of the inactivation data of J. W. Gowen (tobacco mosaic virus). Differences of interpretation of these two sets of experiments carried out with different types of radiation are pointed out.

It is known that experiments on the effect of radiations on microorganisms can be used to determine the volume of the region which must absorb an amount of administered energy in order to produce the observed effect. This volume is the so-called *sensitive volume* and is situated, in general, inside the microorganism. The possibility exists, however, that energy originally absorbed in a medium surrounding the microorganism is conveyed to the latter by various energy transfer processes, so that the size of the sensitive volume involved in a radiation experiment may be larger than the size of the whole microorganism. This is the reason the sensitive volume primarily has a *physical meaning*. The size of the biological entity responsible for the effect observed may be smaller or larger than that volume, since transfer of energy in and outside of the microorganism is possible in all directions. The details of the transfer of energy in this kind of process are not well known; consequently, no definite relations between the two kinds of volumes can be established. If the effect of radiation is primarily due to a chemical reaction, the biological or biochemical sensitive volume may, perhaps, appear in an ultimate analysis as some kind of spheroid whose length is that of a single chemical bond.

When calculating the sensitive volume from the relationship between the frequency of microorganisms showing a given effect and the administered amount of energy we must take into account the density of ionization produced by the type of radiation used. D. E. Lea (1947, pp. 83–7, 353–54) has given an approximate formula which does take this effect into account. It is the purpose of the present note to derive an exact formula and to apply it to a set of experiments on inactivation of the tobacco mosaic virus.

Lea assumes that, if one ion or one cluster of ions occurs in the sensitive volume, this is sufficient to produce the observed effect. The theory leading to an exact expression of his formula can be presented in the following manner: The sensitive volume is assumed to be a sphere of radius r. The probability of occurrence of at least one ion (or of at least one ion cluster) within a length x of a track of an ionizing particle is assumed to be, according to Poisson distribution, equal to:

$$1 - e^{-x/L},$$

where L is the mean distance between two consecutive ions. This formula is, of course, an approximation and does not express the well-known fact that the density of ionization increases as the particle is slowed down in its passage through the matter. The ionizing tracks are not assumed to end within the sensitive volume. The probability of entry of an ionizing particle into, or of its exit out of, the sphere through an infinitesimal surface area is assumed to be proportional to the size of the latter independently of its position. Let us consider the point of entry of the particle into the sphere and the angle between the diameter passing through that point and the track of the particle. The probability that this angle is between ϕ and $\phi + d\phi$ is $\sin 2\phi d\phi$. The length of the corresponding track within the sphere is between $2r\cos\phi$ and $2rd\cos\phi$. Consequently the probability that a particle entering the sphere under an angle of ϕ leaves at least one ion in it is

$$1 - \exp\left[-(2r\cos\phi)/L\right].$$

The probability that a particle entering the sphere under any angle ionizes it at least once is

$$\begin{aligned}\Phi(\xi) &= \int_0^{\pi/2} (1 - e^{-\xi\cos\phi}) \sin 2\phi \, d\phi \\ &= 1 + 2\xi^{-1} e^{-\xi} - 2\xi^{-2}(1 - e^{-\xi}),\end{aligned} \tag{1}$$

where $\xi = 2r/L$. A similar relation shows that the mean length of

a track within the sphere is $4r/3$. Therefore the mean number of ions per track in the sphere is $4r/3L$. If the administered dose is measured as the mean number D of ions per unit of volume, the number of tracks crossing the sphere as a result of a dose D can be taken as:

$$\frac{4}{3}\pi r^3 D \Big/ \frac{4}{3}\frac{r}{L} = \frac{3}{2\xi} vD,$$

where v is the volume of the sphere. Therefore the probability P of ionizing the volume v at least once with a dose D is:

$$P = 1 - (1 - \Phi)^{3vD/2\xi}. \tag{2}$$

Lea's formula is the first order term of equation (2) expanded in power series of Φ. Since

$$\lim_{\xi \to 0} \Phi(\xi) \Big/ \left(\frac{2}{3}\xi\right) = 1,$$

we have $P \to 1 - e^{-vD}$ as $\xi \to 0$, which is intuitive since $\xi = 0$ corresponds to $L = \infty$. Similarly, $P = 0$ for $L = 0$ and $P = 1$ for $D = \infty$. It is seen from equation (2) that $\ln(1 - P)$ is a linear function of the dose D, a property well known in elementary theory where the

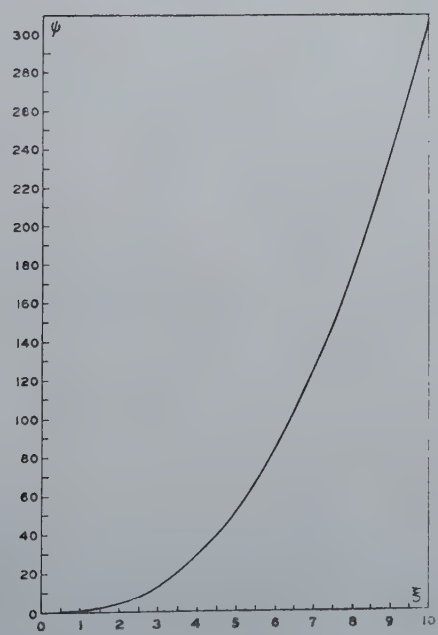

FIGURE 1. The function $\psi(\xi)$ for ξ from 0 to 10.

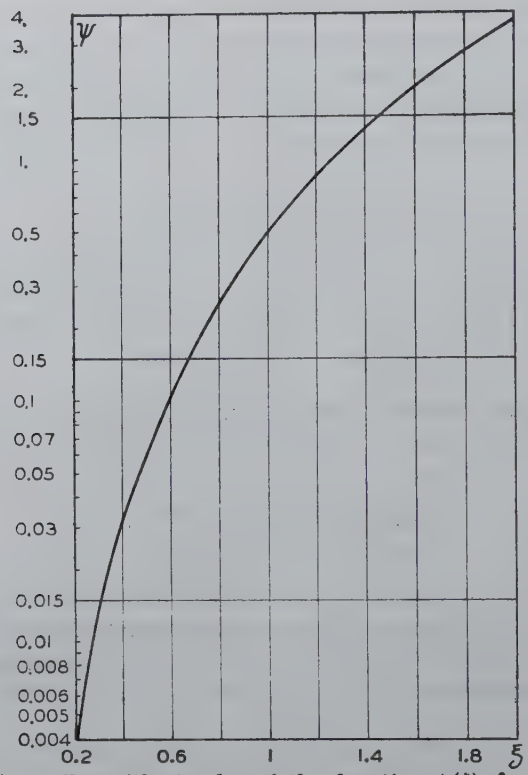

FIGURE 2. A semilogarithmic plot of the function $\psi(\xi)$ for ξ from 0.2 to 2. For $\xi < 0.2$ the effect of ionization density is negligible.

effect of ionization density is neglected ($L = \infty$). Formula (2) can be written also in the form:

$$\ln(1-P) = -\Psi(\xi)L^3D, \tag{3}$$

where $\Psi(\xi) = -(\pi/4)\,\xi^2 \ln(1-\Phi)$. Graphs of the function $\Psi(\xi)$ are given in Figures 1 and 2. For small values of ξ, i.e., for sensitive volumes small with respect to the mean distance of two consecutive ions, we have

$$\Psi(\xi)L^3 = v(1-\xi/24+\cdots) \tag{4}$$

which corresponds to:

$$\Psi(\xi) = (\pi/6)\xi^3(1-\xi/24+\cdots). \tag{5}$$

In these formulae $\xi/24$ represents the correction term due to the ionization density. The corresponding term is $-3\,\xi/8$ in Lea's formula (*loc cit.*, p. 86). For $\xi < 0.2$ we have $1-\xi/24 \approx 1$ with an

error smaller than 2 per cent, and because of formulae (3) and (4) $\Psi(\xi)L^3 \approx v$, $\ln(1-P) \approx -vD$, which means that within this range of ξ the effect of density of ionization is completely negligible. This is intuitive since smaller values of ξ mean that the distance between the ions is large with respect to the diameter of the sensitive volume. For doses of D which are sufficiently small, P is small with respect to unity and we can write, instead of formula (3),

$$P \approx \Psi(\xi)L^3D\,. \tag{6}$$

The formula given by Lea is (*loc. cit.*, p. 353):

$$P = (\pi/6)\xi^3L^3D/F\,, \tag{7}$$

where he has tabulated $F = 2\xi/(3\Phi)$. For $\xi = 1$ and $\xi = 10$ formula (6) gives $P \approx 0.5\ L^3D$ and $P \approx 307\ L^3D$ respectively, whereas Lea's formula (7) gives $P = 0.37\ L^3D$ and $P = 77\ L^3D$. Thus the difference between the two formulae is substantial even for very small doses. The difference is more pronounced with high ionization densities, since then L is small and ξ is large. The proportionality between P and D involved in Lea's formula holds theoretically only for an infinitesimal dose D.

The determination of the sensitive volume from experimental data can be carried out in the following manner: The value of L is known from the type of radiation used. Then a semilogarithmic plot of $1-P$ against D, using formula (3), gives us the value of Ψ. From Figure 1 or 2 the corresponding value of $\xi = 2r/L$ is obtained, which gives the diameter $2r$ of the sensitive volume. This procedure was applied to a set of J. W. Gowen's (1940) experimental data on inactivation of the ordinary strain of the tobacco mosaic virus by three different wave lengths of x-rays. A semilogarithmic plot of the number of surviving viruses is linear, as required by equation (3), except at very high doses. This deviation from linearity may be due to the fact that at high doses a substantial fraction of viruses undergoes non-lethal mutations which are not taken into account in the above plots. Consequently the theory was applied to the linear part of the diagrams which cover about 500,000 roentgen for $\lambda = 1.5$ and 2.1 A°,and almost the full range of the dose for $\lambda = 0.7$ A°, since the deviation from linearity in this latter case is quite small. The conversion of the dose in roentgen to a dose expressed as a number of ions per cubic micron has been made on the assumption of 1.5 ions per μ^3 according to the calculations of Lea (*loc. cit.*, p. 8) for virus protein. The average energy of the electrons ejected by the photons of 0.7, 1.5, 2.1 A° has been assumed to be respectively 14.2, 7.7, 5.7

KeV (cf. Lea *loc cit.*, p. 12). Accordingly the mean distances L between the ions have been taken to be 446, 265, 202 A° (cf. Lea, p. 25). This gives us the following result:

λ A°	Ψ	ξ	$2r$ in $10^{-2}\mu$
0.7	0.12	0.62	2.76
1.5	0.15	0.68	1.83
2.1	0.17	0.69	1.39

Although not very large, there is a systematic deviation from the theory since the latter requires a constant $2r$. Possible reasons for this deviation are: (a) too crude a calculation of the mean distance L between the ions, and (b) the fact that the wave lengths upon which the calculations are based are only *average* wave lengths. The average size of the sensitive volume as given by Gowen (*loc. cit.*) corresponds to $2r = 2.43 \times 10^{-2}\mu$. This magnitude does not take the ionization density into account, whose effect with the present wave length of x-rays is small in any event.

If we disregard the effect of ionization density, that is, if we calculate v from the formula

$$P = 1 - \exp(-vD),$$

we obtain practically the same v as if we take this effect into account. Independent of any physical interpretation of the coefficient v in the above formula for P, it is clear that v is a measure of the inactivating efficiency of the radiation, since a small v corresponds to a small P for the same dose D. The quantity v is proportional to the cube of the calculated diameters. Therefore, in the experiments discussed, the inactivating efficiency of the radiation decreases very strongly with the increase of the wave length. If the assumptions of the present calculations are correct, this change in efficiency cannot be explained by the purely geometrical fact that the ions are closer to each other when the wave length is longer, so that in the latter case the probability is higher that within the sensitive volume more ions will occur than are required for inactivation. There is, of course, the possibility, which we do not analyze here, that when the ions are closer to each other, there is more likelihood for the products of ionizations to recombine with each other and to restore the irradiated molecules to their original form in this way. It is conceivable that such recombination phenomenon may decrease the efficiency of radiation with the increase of the wave length.

We close this note by pointing out that, if absorption of a photon

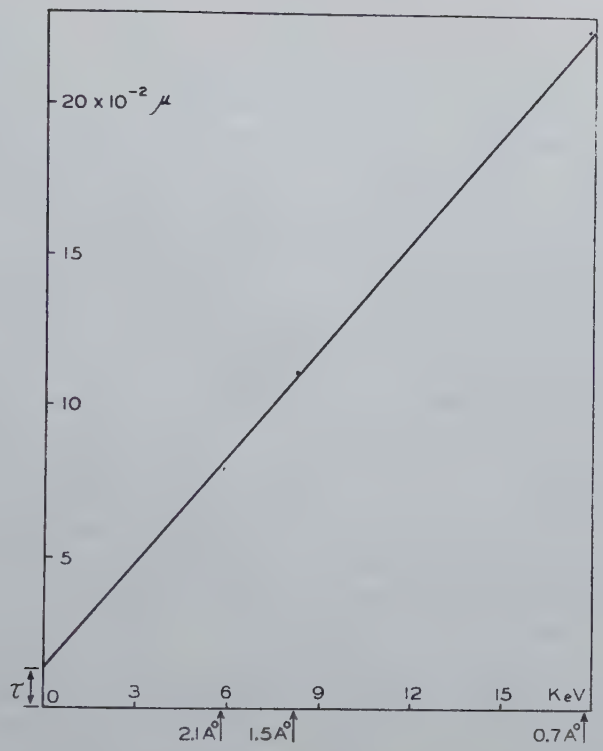

FIGURE 3. Linear relation between the calculated apparent diameter of the sensitive volume and the energy of the photon. Inactivation data of Gowen (*loc. cit.*) on the normal strain of the tobacco mosaic virus. τ indicates a possible true diameter of the sensitive volume, according to a theoretical interpretation of the diagram.

rather than of a single ionization is considered as the event leading to the inactivation of the virus, a linear relation between the diameter of the sensitive volume v_p and the energy of the photon is obtained. Figure 3 represents such a linear relation obtained from Gowen's data for the tobacco mosaic virus. The size of v_p has been calculated by means of the formula

$$1 - P = \exp\,(-v_p D_p), \tag{8}$$

where D_p is the dose measured as the average number of photons per cubic micron. The conversion to D_p of the dose measured as number D_i of ions per cubic micron has been carried out by means of the formula $D_i = h\nu D_p/\varepsilon$, where $h\nu$ is the energy of the photon and ε the average energy spent per ion. The value of 32.5 eV which has been taken for ε is the currently used average energy per ion in the case of air (Lea, *loc. cit.*). The use of this value of ε for virus is further justified by the fact that 44 different sets of measurements on 29 gases and 1 liquid (Compton and Allison, 1946, p. 478; Mohler and Taylor, 1934; Thomson, 1933, p. 238) gave a value of ε from 0.77

to 1.54 times smaller than in air with a mean of 1.2; the value of ε found for air in most of these sets of experiments was 36.4 eV (measurements of Gaertner, cf. Compton and Allison, *loc. cit.*).

A linear relation between the calculated diameter of the sensitive volume and the energy delivered by the primary particle per unit length of its track has been observed by E. C. Pollard and F. Forro, Jr. (1949). These authors explain this fact by assuming that the energy delivered by a particle along its track is transferred radially from it at such a rate that the energy available in the medium per unit volume is inversely proportional to the distance from the particle track. Pollard and Forro suggest that a certain amount of this energy must be absorbed by the sensitive volume of the microorganism to produce its inactivation. This energy has, according to their experiments, the character of an activation energy of a chemical reaction. It equals 3.2 eV for the $T - 1$ phage and has been known to be 1.5 eV for mutations of Drosophila (Timoféeff-Ressovsky, 1937). Pollard and Forro associate with each particle a *"volume of action"* which is characterized by the fact that sufficient energy is available for inactivation inside but not outside of its boundaries. This volume of action, which could also be called an *apparent sensitive volume,* is fundamentally a purely physical concept. It is this volume which, according to Pollard and Forro, is directly calculable from relation (8).

On the basis of these concepts Pollard and Forro reach the conclusion that the diameter of the true sensitive volume can be obtained from the above-mentioned linear relation as the apparent diameter which corresponds to a zero energy of the particle. They find in this way a diameter of the true sensitive volume of $2.8 \times 10^{-2}\mu$ for the $T - 1$ phage. The diagram of Figure 1 would give a true diameter of $1.3 \times 10^{-2}\mu$ for the tobacco mosaic virus. J. W. Gowen (*loc. cit.*) has also given inactivation data for the Aucuba and an ADO variant of the tobacco mosaic virus. If these are analyzed in a similar manner as has been done for the normal strain of the tobacco mosaic virus, a somewhat smaller, but still quite good, linear relation between the calculated apparent diameters and the energy of the photon is obtained. The true diameters obtained by this analysis are found to be about twice as large as for the normal strain of the tobacco mosaic virus, bringing the average size of the true sensitive volume of these three variants very close to that found by Pollard and Forro for the $T - 1$ phage.

Perhaps the exact statistical relation between the apparent and

the true sensitive volumes should be investigated more carefully than it has been up to now. Although the conditions of the two sets of experiments are very different from each other, since Pollard and Forro used heavy particles of few MeV and in Gowen's experiments the ionizing particles were mainly photoelectrons of some 5 to 15 KeV, the linear relationship noted in both cases suggests possible similarities of the fundamental physico-chemical mechanisms in both cases. In evaluating this possibility one should keep in mind the fact that Pollard and Forro found a linear relation between the diameters of the sensitive volumes and the dose delivered per unit length of track of the primary particle, whereas the present analysis indicates a linear relationship between the diameters and the energy absorbed per photon. If the basic mechanisms of inactivation are similar in both cases, that difference may be due, perhaps, to purely physical differences in the manner in which the energy of x-rays and deuterons is absorbed by the irradiated medium.

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LITERATURE

Gowen, J. W. 1940. "The size of the tobacco mosaic particle from x-ray determination." *Proc. Nat. Acad. Sci.*, **26**, 8–10.

Lea, D. E. 1947. *Actions of Radiation on Living Cells.* Cambridge: University Press.

Compton, A. H. and S. K. Allison, 1946. *X-rays in Theory and Experiment.* New York: Van Nostrand.

Mohler, F. L. and L. S. Taylor, 1934. "Ionization of Liquid Carbon Disulphide by X-rays." *Nat. Bur. of Standards Jour. of Res.*, **13**, 659–64.

Thomson, J. J. and G. P. Thomson. 1933. *Conduction of Electricity Through Gases.* Vol. 2. Cambridge: University Press.

Pollard, E. C. and F. Forro, Jr. 1949. "Examination of the Target Theory by Deuteron Bombardment of *T* — 1 Phage." *Science*, **109**, 374–75.

Timoféeff-Ressovsky, N. W. 1937. *Experimentelle Mutationsforschung in der Vererbungslehre.* Dresden: T. Steinkopf.

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DIFFUSION AND RECOMBINATION OF PRODUCTS OF IONIZING RADIATIONS

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The relative importance of diffusion and recombination of the products of ionizing radiations is examined in several typical cases and methods for the solution of the differential equation of columnar ionization are discussed. It is shown that Jaffé's method is not applicable to radiobiological or purely radiochemical processes in which no external electric fields are acting. A method based on a recent suggestion of Kramers (see Gerritsen, 1948) appears to be particularly good when recombination is strong.

1. *The background and the objectives of the paper.* The fact that the amount of energy needed to produce a given biological effect depends on the energy of the ionizing particle has been noted in many cases (cf. Lea, 1946; Timoféeff-Ressovsky and Zimmer, 1947). The type of experiment in which the efficiency of the radiation is measured as the number of microorganisms showing a certain effect per unit amount of administered energy is particularly appropriate for quantitative discussions. Theories have been suggested to explain this so-called wave length dependence of the biological effects of radiations. This can show two opposite types of relation: the biological efficiency of a radiation may increase or decrease with the increase of density of ionization. We are concerned here with the latter type of effect (for examples of the former see, e.g., Failla, 1949; Zirkle, 1935). Among the earliest theories suggested to explain this wave length effect is one based on the concept of sensitive volume in which an ionization should occur to initiate a biological process. According to this theory an increase of the wave length of radiation may decrease its efficiency, because with an increase of the wave length the density of ionization increases and, consequently, there is more chance that if a sensitive volume is ionized at all it is ionized more than once. Some experimental results are in agreement with this theory (cf. Lea, 1946). However, examples are known (see, e.g., Opatowski, 1951) in which the effect of wave length as calculated by

the theory mentioned above appears completely negligible, whereas the experiment shows a very marked magnitude of this effect. Two theories can be considered to explain this and other disagreements. One may be based on a recent suggestion of E. C. Pollard and F. Forro (1949) (cf. Opatowski, 1951) which combines the concept of activation energy of a biological process with that of transport of energy delivered by the primary particle to the medium surrounding the sensitive volume. This leads to the concept of a sphere or volume of action of the primary particle which depends on the energy of the latter and is, in general, larger than the biological sensitive volume. The other theory considers a chemical or ionic recombination of the direct or indirect products of the ionizing radiation (cf. Lea, 1946, 1947). This recombination may concern the positive and negative ions produced by the radiation or some groups of atoms produced by the ions. With densely ionizing radiations the ions and their products are closer to each other, so that the chance for their recombination is higher which would decrease the efficiency of a densely ionizing radiation. There are several complications which make a quantitative evaluation of this latter theory difficult. First of all, with the exception of some simple radiochemical reactions, the exact nature of the processes induced by radiation is not known. This lack of sufficiently accurate quantitative knowledge unfortunately pertains to water also, an important substance from a biological viewpoint (a discussion of this subject with extensive bibliographical references can be found in Toulis, 1950). Second, the process of recombination is superimposed upon a concomitant process of diffusion. Thus their quantitative aspects have to be studied on the basis of the theory of diffusion with the addition of the kinetics of recombination, which introduces a nonlinear term into the differential equation of diffusion.

Notwithstanding the phenomenological uncertainties of the field and its theoretical difficulties, attempts have been made to apply the theory last mentioned to concrete questions of importance for an understanding of some radiobiological processes (see Lea, 1947). The mathematics used therein was based on a semi-empirical method of Jaffé (1913) for the solution of the diffusion-recombination equation. This method has been applied several times since its first publication, but mainly for gases and only in the presence of external electric fields. It is shown in the present paper that in the absence of these fields Jaffé's method leads to an inacceptable conclusion. Recently A. N Gerritsen (1948) noted that an application of Jaffé's method for liquids, even in the presence of external electric fields, may lead

to errors. H. A. Kramers suggested a new method to replace Jaffé's. A perturbation method was given by H. G. Landau (1950). These various methods, together with two new ones, are examined in the present paper with particular reference to phenomena in liquids in view of their importance in biology.

The mathematical nature of the problem can be presented in its simplest possible form by considering the particular case in which the recombining ions or groups of atoms have the same diffusion coefficient D. Then, if n is their concentration and t the time, we have:

$$\partial n/\partial t = \text{divgrad}\, n - \alpha n^2, \tag{1}$$

where α is a constant characterizing the time rate of recombination. Jaffé assumed that a short time after the passage of the ionizing particle the ions or the groups of atoms formed by the latter were distributed at random around the track of the primary particle. Accordingly, he gives

$$n(r, 0) = N_0 (\pi b^2)^{-1} \exp(-r^2/b^2) \tag{2}$$

as the initial condition for the function $n(r, t)$, where r is the distance from the primary track and N_0 and b are two constants. If n is measured as the number of ions (or groups of atoms) of each kind per unit volume and l is the length of the primary track, $N_0 l$ is the total number of ions of each kind at $t = 0$. Their mean distance from the axis of the primary track is $b\sqrt{\pi}/2$. Expression (2) has to be interpreted as an *average* concentration along the track, since n is actually smaller at the beginning than at the end of the track.

2. *The relative importance of diffusion and recombination.* Since equations (1) and (2) cannot be solved in finite terms, it is important to estimate the relative order of magnitude of the two terms on the right-hand side of equation (1) before choosing an appropriate approximate method of solution. It appears from Gerritsen's work that for α-particles in liquids the recombination term αn^2 predominates over the diffusion term D divgrad n. But Gerritsen experimented at very low temperatures (liquid N,H,He,A); at room temperature the diffusion coefficient is likely to be much higher and no direct conclusion, for this temperature, can be drawn from his work. However, at $t = 0$ we have:

$$K = \frac{D\, \text{divgrad}\, n}{\alpha n^2} = \frac{4\pi D}{\alpha N_0}\left(\frac{r^2}{b^2} - 1\right) \exp \frac{r^2}{b^2}, \tag{3}$$

which expresses the relative contribution of diffusion and of recom-

bination processes to the change of concentration at r. It is seen that diffusion initially decreases the local concentration within $r < b$, and thus cooperates with the recombination process; for $r > b$ the opposite occurs. Both regions are important since at $t = 0$ the cylinder $r \leq b$ contains only $1 - e^{-1} \approx 0.63$ of the total number of ions. For brevity we shall refer to the diffusing entities as ions, although they may consist of neutral groups of atoms. Across the cylinder $r = b$ no diffusion occurs at $t = 0$. The total number of ions which at $t = 0$ are outside of the cylinder $r = b$ is $N_0 \exp(-r^2/b^2)$.

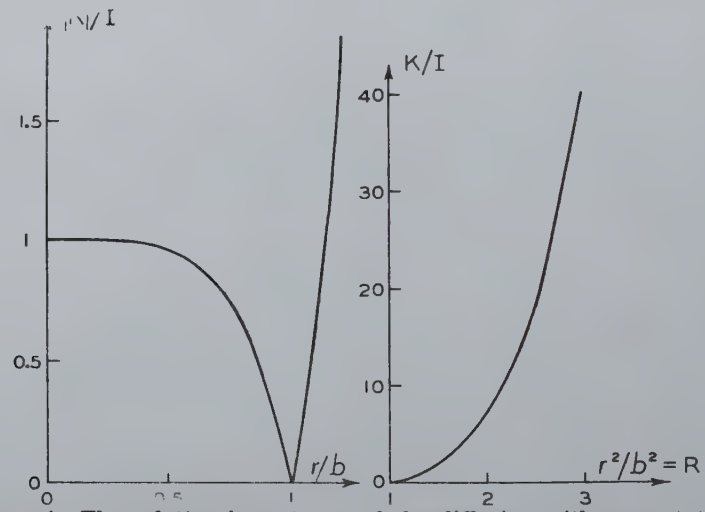

FIGURE 1. The relative importance of the diffusion with respect to the recombination process immediately after the passage of an ionizing particle, at various distances from its track. Ordinate $= |K|$ or K in units of $I = 4\pi D/(\alpha N_0)$. Abscissa $= r$ in units of b or r^2 in units of b^2.

Figure 1 gives two graphs of the function K. This function is practically constant within $r < b/2$ and changes very rapidly beyond that, tending to ∞ as $r \to \infty$. Thus sufficiently far from the primary track the concentration of ions is so small that their chance for recombination is practically zero.

The relative importance of diffusion with respect to recombination is initially proportional to

$$I = \phi/N_0, \quad \text{where} \quad \phi = 4\pi D/\alpha. \tag{4}$$

Various theoretical expressions for the quantity ϕ can be given.

We may use the relation $D = kTu$ (valid for perfect gases and based on Fick's law of diffusion), where u is the mobility (velocity acquired under the action of a unit force), k Boltzmann's constant,

and T the absolute temperature. We may consider together with the above Langevin's relation between recombination rate of ions and their mobilities u_+, u_- (see, e.g., Cobine, 1941, p. 99):

$$\alpha = 4\pi e^2 (u_+ + u_-)/\varepsilon ,$$

where e is the ionic charge and ε is the dielectric constant. Then the following formula is obtained for ϕ with the assumption of equal mobilities of both ions:

$$\phi = kT\,\varepsilon/(2e^2) \approx 300T\,\varepsilon . \qquad (5)$$

This formula would indicate a much higher importance of diffusion in water than in gases, because of the high dielectric constant of water. It would also indicate that the importance of diffusion with respect to recombination increases in direct proportion to the absolute temperature. Both these facts suggest that Gerritsen's conclusions derived at very low temperatures for liquid gases, for which $\varepsilon \approx 1$, may not apply to water at room temperature. In fact, in this latter case ϕ would be at least between 10^3 and 10^4 times larger than in his experiments. In addition to this, formula (5) concerns a *purely ionic type of recombination.*

For processes between *neutral groups of atoms* the classical Arrhenius equation or the quantum theory of rate processes (Glasstone, Laidler and Eyring, 1941) or other theories of diffusion (Barrer, 1941) and reaction rates (Moelwyn-Hughes, 1940, p. 537) lead to an expression of the type $A \exp(-E/kT)$ for both D and α, where E is an activation energy and A a constant which may depend on T. In the simplest case in which A is for both processes either independent of T or dependent on it in the same manner, the factor ϕ and, consequently, the relative importance of diffusion with respect to recombination, would decrease with increasing temperature if the activation energy for recombination is higher than for diffusion. This is an opposite type of relation than that expressed by equation (5) for purely ionic recombinations. It may be expected to occur frequently since activation energies for diffusion in liquids are relatively small.

The dependence of diffusion and recombination on the type of radiation used is expressed in K through the density of ionization N_0. The lower this density, the more important is diffusion with respect to recombination. From a theoretical viewpoint one would expect that b also depends on the type of radiation since it is proportional to the mean distance of ions from the primary track. Higher energy particles produce δ-rays of longer range; consequently, one would expect that b should increase with increasing energy of the

TABLE I

The values of $I = \phi/N_0$ express the relative importance of diffusion with respect to recombination at the primary track ($r = 0$) in tissue, water, and air, for various types of radiation a very short time after the passage of the primary particle or photon ($t = 0$).

The number of ions per micron of path is taken from L. H. Gray (1947) for tissue and calculated for air according to the relation: (number of ions per cm of path in air at NTP) ≈ 12 (number of ions per micron of path in wet tissue). This approximate formula is based on the assumption that the number of ions per unit length of path is proportional to the number of electrons per cm^3 of the medium and that the number of electrons, referred per unit mass, is 10% higher in wet tissue than in air (Lea, 1946, p. 347).

The values used of the diffusion and recombination coefficients for H and OH in water,

$$D = 5 \times 10^{-5}\ \mathrm{cm^2/sec}\,, \quad \alpha = 4 \times 10^{-10}\ \mathrm{cm^3/sec}\,,$$

are approximately the average values suggested by Lea (1947). The above value of D is very close to the mean diffusion coefficient of H^+ and OH^- as calculated from their mobilities in water. In fact, since $\nu_+ = 3.242 \times 10^{-3}\ \mathrm{cm^2/(sec\ Volt)}$ and $\nu_- = 1.802 \times 10^{-3}\ \mathrm{cm^2/(sec\ Volt)}$ (see Creignton, 1943, p. 133), we have, using $\nu = (\nu_+ + \nu_-)/2$,

$$D = 300\nu kT/e \approx 6.5 \times 10^{-5}\ \mathrm{cm^2/sec}\,.$$

For air the values used of

$$D = 3.7 \times 10^{-2}\ \mathrm{cm^2/sec}\,, \quad \alpha = 1.67 \times 10^{-6}\ \mathrm{cm^3/sec}$$

are Jaffé's experimental values (1929). This α is identical with $1.71 \times 10^{-6}\ \mathrm{cm^3/sec}$ given by K. T. Compton and I. Langmuir (1930, p. 194) and D is quite close to the magnitude obtainable from the average mobilities of air ions. In fact, since $\nu_+ = 1.58$ and $\nu_- = 2.3\ \mathrm{cm^2/(sec\ Volt)}$ (cf. Cobine, 1941, p. 38), the above relation between D and ν gives us $D \approx 5 \times 10^{-2}\ \mathrm{cm^2/sec}$.

The temperature is assumed to be $T = 300°$; the dielectric constant for wet tissue the same as for water: $\varepsilon = 81.7$. Monovalent ions are assumed in calculations.

The quantity d gives the percentage of the total number of ions for which the effect of diffusion exceeds the effect of recombination at $t = 0$, i.e., a short time after the passage of the primary particle. It is calculated by the formula:

$$d = \exp(-R_1), \text{ where } (R_1 - 1)\exp R_1 = 1/I .$$

R_1 is the root of equation (3) in which $R = r^2/b^2$ is considered as the unknown and $K = 1$. Values of R_1 can be taken directly from the curves of Figure 1 which represents $(R - 1)\exp R$.

TYPE OF RADIATION	SOFT TISSUE or WATER		AIR AT *NTP*	
	ionic recombinations, calculations based on Langevin's formula, equation (5)	*chemical recombination*, H and OH in water, calculations based on equation (4)	*ionic recombination*, calculations based on: Langevin's formula, equation (5)	Equation (4)
2 MeV γ-rays ($\sim$ 0.006 Å), $\sim$ minimum ionization density obtainable with any kind of radiation (Gray, 1947)	$N_0 \approx 6.3$ ion pairs per micron		$N_0 \approx 75.6$ ion pairs per cm	
	$I = 117$	$I = 25$	$I = 1190$	$I = 3683$
	Recombination process initially completely negligible with respect to diffusion			
2 Å X-rays or $\sim$ 6KeV β-particles (cf. Lea, 1946, pp. 12, 24)	$N_0 \approx 100$ ion pairs per micron		$N_0 \approx 1200$ ion pairs per cm	
	$I = 7.35$	$I = 1.57$	$I = 75$	$I = 232$
	Recombination initially small with respect to diffusion		Recombination initially negligible with respect to diffusion	
$\sim$ 1/2 MeV protons or $\sim$100 eV β-particles	$N_0 \approx 1000$ ion pairs per micron		$N_0 \approx 12000$ ion pairs per cm	
	$I = 0.73$; $d = 26\%$	$I = 0.16$; $d = 15\%$	$I = 7.5$	$I = 23.2$
	Effect of recombination initially predominant		Recombination initially small with respect to diffusion	
$\sim$ 1MeV α-particles, approximately maximum obtainable ion density with particles not heavier than α-particles (Gray, 1947)	$N_0 \approx 5200$ ion pairs per micron		$N_0 \approx 62400$ ion pairs per cm	
	$I = 0.14$; $d = 14\%$	$I = 0.03$; $d = 6\%$	$I = 1.44$	$I = 4.46$
	Effect of recombination initially predominant		Recombination initially small with respect to diffusion	

primary particle. Similarly one would expect that b would be larger for X- and γ-rays than for heavily ionizing particles. However, experimental data on this subject are not available.

Table I gives some numerical information on the relative importance of the diffusion and recombination processes *a very short time after the passage of the particle or photon.* It is seen that the effect of recombination is small in air, but not in water and tissue in the case of heavily ionizing particles. It is noteworthy that none of the conclusions of Table I depend on b, that is, on the radial distribution of ions.

3. *Methods of successive approximations for the solution of the equations.* We now proceed to a discussion of approximate methods of solution of equations (1) and (2). To simplify the formalism we introduce the following symbols:

$$\left.\begin{aligned} &A = 4D/b^2, \quad B = \pi b^2/N_0, \quad g = \alpha/(AB) = 1/I, \\ &R = (r/b)^2, \quad T = At, \quad M = 1 + T, \quad f = Bn. \end{aligned}\right\} \tag{6}$$

Equations (1) and (2) then become, using the assumption of a cylindrical symmetry of n,

$$\frac{\partial f}{\partial T} = \frac{\partial}{\partial R}\left(R\frac{\partial f}{\partial R}\right) - gf^2, \tag{7}$$

$$f(R, 0) = \exp(-R). \tag{8}$$

Or, in the equivalent integral form,

$$f = \int_0^T \left[\frac{\partial}{\partial R}\left(R\frac{\partial f}{\partial R}\right) - gf^2\right] dT + \exp(-R). \tag{9}$$

If recombination predominates over diffusion we can take

$$f_{r1} = 1/(gT + \exp R)$$

as a first approximation to f. The function $f = f_{r1}$ is the solution of equations (7) and (8) when $D = 0$. The next approximation $f = f_{r2}$ is obtained by substituting $f = f_{r1}$ in the right-hand side of equation (9). This gives us:

$$f_{r2} = f_{r1}(1 - T + TRe^R f_{r1}). \tag{10}$$

This process can be continued and the integrations involved in any of the successive approximations can be expressed in finite terms. This is essentially a method suggested by Kramers.

If diffusion predominates over recombination one can proceed in a similar manner. As the first approximation to the function f one can take

$$f_{D1} = M^{-1} \exp(-R/M),$$

which is the exact solution of the system (7)—(8) in the case of zero recombination. Then the next approximation follows from equation (9):

$$f_{D2} = f_{D1} - gF_0(2R,M),$$

where $F_0(2R,M) = (e^{-2R/M} - e^{-2R})/2R$. The function F_0 is one of the following set of functions that we will encounter later:

$$F_n(x, M) = \int_1^M \mu^{n-2} e^{-x/\mu}\, d\mu = M^{n-1} E_n(x/M) - E_n(x),$$

$$E_n(x) = \int_0^1 \mu^{n-2} e^{-x/\mu}\, d\mu .$$

Tables of G. Placzek (1946) are available for the function E_n and from the Mathematical Tables Project (1940) for the exponential integral $E_1(x) = -\operatorname{Ei}(-x)$.

An *intermediate approximation* is obtained if one starts from a suitable combination of f_{D1} and f_{r1} as a first approximation to f. For instance, one can take as such a first approximation:

$$f_{i1} = (1-h) f_{D1} + h f_{r1}, \tag{11}$$

which satisfies equation (8) independently of h. If

$$h = [1 + (R-1) g^{-1} e^R]^{-1},$$

equation (7) is also satisfied at $T = 0$. Equation (9) then gives the next approximation to f:

$$\begin{aligned} f_{i2} = {} & (1-h)(f_{D1} - e^{-R}) + \frac{h}{g}(1 - e^R f_{r1})(Re^R f_{r1} - 1) \\ & + (Rh'' + h')\left[\frac{1}{g}\ln(gT + e^R) - \frac{R}{g} - F_1(R, M)\right] \\ & + 2Rh'\left[F_0(R, M) - \frac{e^R}{g}(e^{-R} - f_{r1})\right] \\ & - g\left[(1-h)^2 F_0(2R, M) + \frac{h^2}{g}(e^{-R} - f_{r1}) \right. \\ & \left. + 2h(1-h)\beta e^{g\beta R} F_1\left(\beta R e^R, \frac{e^R}{g + (\beta M)^{-1}}\right)\right] + e^{-R}, \end{aligned}$$

where $\beta = 1/(e^R - g)$, $h' = dh/dR$, $h'' = d^2h/dR^2$.

4. *A numerical discussion of the successive approximation methods.* Two successive approximations to f are good if they do not differ very much from each other [cf. equation (9)]. Let us consider ions around the primary track ($R = 0$). Since

$$f_{r2}(0, T)/f_{r1}(0, T) = 1 - T,$$

f_{r1} and f_{r2} are good approximations to f for sufficiently small T. Since $t \equiv T/D$, small T means longer time *if diffusion is smaller.* Consider, for instance, the time that would be required to reduce the concentration at $R = 0$ to 10% of its initial value if diffusion were completely negligible. It follows from the expression of f_{r1} that this time would be in dimensionless units $T = 9/g$. Among the examples considered in Table I the one in which the effect of diffusion is the smallest is that concerning H, OH, and 1 MeV α-particles for which $I = 1/g = 0.03$. This would give us $T = 0.27$. Thus within the time considered the error with which $f_{r2}(0, T)$ may be affected can be estimated as being smaller than 27%. According to a suggestion of Lea that $b = 10^{-6}$ cm, we find that $T = 0.27$ corresponds to $t = 1.35 \times 10^{-9}$ sec. For intervals of time twice as large, $f_{r2}(0, T) < 0$, the method fails. The time t that enters into the present theory is not counted from the moment of passage of the particle, but from the moment at which the ions produced by the particle have acquired distribution (2) and have lost so much of their kinetic energy that their motion is subject to the laws of diffusion. It is difficult to estimate this moment in an accurate manner. Landau (1950) shows that if the energy of the primary particle is absorbed instantaneously it takes $b^2/4D$ sec for the ions to acquire distribution (2) under the assumption that recombination has not acted during this time. With the values of constants used here that time would be 5×10^{-9} sec. Perhaps a more informative comparison is obtained if, instead of local concentrations, the total number of ions (or atom groups) is considered. This number, expressed as a fraction of the total number initially present, is:

$$N(t)/N_0 = \int_0^\infty f(R, T)\,dR = [\ln(1 + gT)]/(gT)$$

in *both first and second approximations,* i.e., using f_{r1} or f_{r2} for f. This is to some extent intuitive, since diffusion, which the method treats as a second order effect, changes the distribution of the ions but not their total number. In the numerical example just consid-

ered when the concentration at the primary track is somewhere between ~ 0.075 and 0.1 of its initial value, the total number of ions is reduced to ~ 0.26 of their initial number, according to the above formula, independent of the value of b, whose only effect is to fix the scale of length and of time. In the third approximation we have from equation (9)

$$N(t)/N_0 = \int_0^\infty f_{r3} dR = 1 - g \int_0^\infty dR \int_0^T f_{r2}^2 dT,$$

because $R\partial f_{r2}/\partial R$ is zero for both $R = 0$ and $R = \infty$. Taking equation (10) into account we have:

$$\int_0^\infty dR \int_0^T f_{r2}^2 dT = \int_0^T (1-T)^2 dT \int_0^\infty f_{r1}^2 \, dR$$
$$+ 2 \int_0^T T(1-T) dT \int_0^\infty R e^R f_{r1}^3 dR$$
$$+ \int_0^\infty R^2 e^{2R} dR \int_0^T T^2 f_{r1}^4 dT.$$

If we put $gT = \tau$ and use the substitution $\tau + e^R = u$, we find:

$$\int_0^\infty f_{r1}^2 dR = 2 \int_0^\infty R e^R f_{r1}^3 dR = \frac{1}{\tau}\left[\frac{\ln(1+\tau)}{\tau} - \frac{1}{1+\tau}\right],$$

$$\int_0^\infty R^2 e^{2R} dR \int_0^T T^2 f_{r1}^4 \, dT = \frac{T^3}{3} \int_0^\infty \frac{R^2 e^R dR}{(gT + e^R)^3} = \frac{T^3}{3} \int_1^\infty \frac{(\ln w)^2}{(w+\tau)^3}$$
$$= \frac{T^3}{6\tau}\left(\frac{J}{\tau} - \frac{\partial J}{\partial \tau}\right)_{w=1}^{w=\infty},$$

where $w = e^R$,

$$J = \tau \int \frac{(\ln w)^2}{(w+\tau)^2} dw = 2\mathrm{L}\left(1 + \frac{w}{\tau}\right)$$
$$+ \left[\frac{w \ln w}{w+\tau} - 2\ln\left(1 + \frac{w}{\tau}\right)\right] \ln w,$$

L being a tabulated function (see Fletcher, Miller and Rosenhead, 1946, pp. 343-44; Powell, 1943; Fletcher, 1944) defined by

$$\mathrm{L}(x) = \int_1^x \frac{\ln \xi}{\xi - 1} d\xi.$$

Taking into account that (Powell, *loc. cit.*)

$$\lim_{x\to\infty} [\mathrm{L}(x) - \tfrac{1}{2}(\ln x)^2] = \frac{\pi^2}{6}$$

we find $J_{w=\infty} = (\pi^2/3) + (\ln \tau)^2$. From this, using the relation (Powell, *loc. cit.*)

$$2\mathrm{L}\left(1 + \frac{1}{\tau}\right) = \frac{\pi^2}{3} + (\ln \tau)^2 - 2\mathrm{L}(1 + \tau),$$

we obtain:

$$\int_0^\infty R^2 e^{2R} dR \int_0^T T^2 f_{r1}{}^4 dT = T[\mathrm{L}(1 + \tau) - \ln(1 + \tau)]/(3g^2).$$

Finally, for the total number of ions in the third approximation we have:

$$\frac{N(t)}{N_0} = \frac{\ln(1 + \tau)}{\tau} + \frac{1}{g}\left(1 - \frac{T}{3}\right)[\mathrm{L}(1 + \tau) - \ln(1 + \tau)]. \quad (12)$$

The first term on the right-hand side of this equation is identical with the expression of $N(t)/N_0$ in the case of pure recombination. Thus the term containing $1/g$ represents the effect of diffusion. Through approximate calculations based on Lea's estimates we found that the total number of H and OH produced in water by a 1 MeV α-particle would be reduced to 26% of their initial number within $t \approx 1.35 \times 10^{-9}$ sec if diffusion were absent. Carrying out calculations with formula (12), which takes diffusion into account, we find that fraction to be ~ 30.5%. (In evaluating the meaning of these figures one should keep in mind that $t = 0$ corresponds to a time which is somewhat later than the moment of passage of the particle.) For large T's formula (12) fails because it gives $N(t)/N_0 < 0$. It is not difficult to derive a third approximation formula also for the concentration at $R = 0$. From equation (9) we have:

$$f_{r3}(0, T) = 1 + \int_0^T \left[\frac{\partial f_{r2}}{\partial R} - g f_{r2}{}^2\right]_{R=0} dT$$

$$= 1 - \frac{1}{g^2}\left[\frac{(g^2 + g + 2)}{1 + \tau} - 2\ln(1 + \tau)\right].$$

Carrying out calculations with the data just considered (1 MeV α-particle in water), one finds the following: Recombination alone would reduce the concentration at the primary track at $T = 0.27$ to

10% of its initial magnitude; taking diffusion into account would give a concentration of 7.3% by the first iteration formula and 7.55% by the next one, just derived for f_{r3}. The closeness of these two last figures speaks well for a good convergence of the method. The relatively small contribution of the diffusion process to the reduction of concentration at the primary track is in agreement with the results of Table I.

If *recombination is small with respect to diffusion* we have at the primary track:

$$f_{D2}(0, T) = M^{-1} - g(1 - M^{-1}).$$

A first limitation to the applicability of this formula is that $f_{D2}(0, T)$ be > 0, which requires $T < 1/g$. This also appears from the ratio:

$$f_{D2}(0, T)/f_{D1}(0, T) = 1 - gT. \tag{13}$$

In the case of a complete absence of recombination, the concentration at $R = 0$ is reduced to 10% of its initial value at $T = 9$ and to 1% at $T = 99$. This can be easily derived from the expression of $f_{D1}(0, T)$. For 2 MeV γ-rays, using Jaffé's experimental data for air, these values of T correspond to $gT = T/I = T/3683 = 2.4 \times 10^{-3}$ and 2.7×10^{-2} respectively. Thus in this case the method would seem very good, as far as the concentration around the primary track is concerned. Its disadvantage is that the second order approximation does not reveal any reduction in the total number of ions, and the third order approximation is difficult to calculate. The previous method would give $N(t)/N_0 = 98\%$ in the present case using formula (12) for $T = 9$. Thus with 2 MeV γ-rays in air diffusion is so strong that ions at the primary track are reduced to a small fraction of their initial number therein during a time when ionic recombination has almost not yet taken place. For $T = 99$ formula (12) fails because it gives $N(t) < 0$; the method over-emphasizes recombination.

The disadvantage of the *intermediate* method is that the calculation of the total number of ions requires involved numerical integrations. At $R = 0$,

$$f_{i1}(0, T) = 1/[(1 + T)(1 + gT)],$$

$$f_{i2}(0, T) = f_{i1}(0, T) + \frac{gT}{1 + gT}$$

$$- \frac{g}{(1-g)^2}\left[\frac{T}{1+T} + \frac{g^2T}{1+gT} + \frac{2g}{1-g}\ln\left(g + \frac{1-g}{1+T}\right)\right].$$

Thus at the primary track this method represents the concentration as the product of the concentrations that would exist there if diffusion and recombination were acting separately.

5. *Comparison with other known methods.* Jaffé (1913) gave a semi-empirical solution of equations (7) and (8) which is:

$$f = \frac{1}{M} \frac{\exp(-R/M)}{1 + (g/2)\ln M}.$$

The use of this solution is equivalent to changing g in equation (7) to $(g/2)\exp(R/M)$. Thus at $R = 0$ only 50% of the effect of recombination is taken into account. Since diffusion is taken into account to its full extent, the error is more pronounced when recombination is strong, which is in agreement with Gerritsen's observations. However, even when recombination is small with respect to diffusion Jaffé's method does not yield the correct order of magnitude of the total number of ions. One can see this by considering Jaffé's formula:

$$N(t)/N_0 = [1 + (g/2)\ln M]^{-1}.$$

Keeping in mind that $g = 1/I$, the time necessary to reduce the total number of ions to 10% of their initial number is, according to the above formula, equal to $T = \exp(18I) - 1$. Using Jaffé's experimental data for air this time becomes in absolute units in the case of 1 MeV α-particles (see Table I; $b = 1.79 \times 10^{-3}$ cm, $A = 4.62 \times 10^4$ sec^{-1}):

$$t = [\exp(18 \times 4.46) - 1]/A \approx 5 \times 10^{22} \text{ years !}$$

As high as this time is, the formula would make it still higher for X- and γ-rays. This shows how misleading an application of Jaffé's theory may be when no electric fields are present. (In all experiments in which Jaffé's theory was used, ions were subject to an external electrostatic field, and no such serious contradictions with the theory have been noted.)

The method of Landau (1950) amounts to expanding f in power series of g. At $R = 0$ his solution is:

$$f(0; T) = \sum_{m=0}^{\infty} g^m f_m(0, T)$$

where $f_0(0, T) = 1/M$,

$$f_1(0, T) = -[\ln(2M - 1)]/(2M),$$

$$2Mf_2(0,T) = \mathrm{L}\left(1-\frac{2}{3M}\right) - \mathrm{L}\left(1-\frac{1}{M+\sigma}\right)$$
$$-\mathrm{L}\left(1-\frac{1}{M-\sigma}\right) + \mathrm{L}\left(\frac{M+\sigma-1}{\sigma-M}\right) + \mathrm{L}\left(\frac{\sigma-M+1}{\sigma+M}\right)$$
$$-\mathrm{L}\left(\frac{2}{M}-3\right) - \ln 3 \cdot \ln M - L(1/3) + (\pi/2)^2,$$

with $\sigma = \sqrt{M^2 - (M/2)}$ and L the function that we have already encountered. (In using Powell's tables for it the formula

$$\mathrm{L}(-y) = \ln y \cdot \ln(1+y) - \mathrm{L}(1+y) - (\pi^2/6)$$

is helpful.) This method requires that either g or T, or both, be sufficiently small; otherwise $f_0 + gf_1$ would be < 0. The method has a disadvantage similar to Jaffé's. The total number of ions up to the terms of first order of this method is $1 - (g/2)\ln M$. Using the same example as in discussing Jaffé's theory we find that it would take a time $T = e^{37} - 1$ to reduce to 10% the total number of ions produced in air by an 1 MeV α-particle. This is an inacceptable result for the same reasons as before. The situation is not improved by considering terms of 2nd order in the expression of $N(t)/N_0$. Although this method is not appropriate for calculating the total number of ions it yields convergent results for concentrations around the primary track if $g << 1$. For instance, for the previously encountered value of $T = 9$, i.e., $M = 10$, we have

$$f(0,T) = 0.1 - 0.147g + 0.433g^2 + \cdots.$$

LITERATURE

Barrer, M. 1941. Diffusion in and through solids. Cambridge: University Press.

Cobine, J. D. 1941. Gaseous Conductors. New York: McGraw-Hill.

Compton, K. T. and I. Langmuir. 1930. "Electrical Discharges in Gases." *Rev. Mod. Physics*, **2**, 123–242.

Creighton, H. J. 1943. Electrochemistry. Vol. I. New York: John Wiley and Sons.

Failla, G. 1949. "Biological Effects of Radiation and Health Protection." *Nucleonics*, **4**, 42–4.

Fletcher, A. 1944. "Note on tables of an integral." *Philos. Mag.*, **35**, 16–17.

———, Miller, J. C. P. and L. Rosenhead, 1946. *An index of mathematical tables.* New York: McGraw Hill.

Gerritsen, A. N. 1948. "Ionization by Alpha-Particles in liquids at low temperatures." *Physica*, **14**, 381–424.

Glasstone, S., K. Laidler, and H. Eyring. 1941. Theory of rate processes. New York: McGraw-Hill.

Gray, L. H. 1947. "The distribution of the ions resulting from the irradiation of living cells." *Brit. Jour. Radiol. Suppl.*, No. 1, 7–15.

Jaffé, G. 1913. "Zur Theorie der Ionisation in Kolonnen." *Ann. d. Physik*, **42**, 303–41.

———. 1929. "Kolonnenionisation in Gasen bei erhöhtem Druck." *Physik. Z.*, **30**, 849–56

Landau, H. G. 1950. "A problem in radiobiology: diffusion and recombination of ions." *Bull. Math. Biophysics*, **12**, 27–34.

Lea, D. E. 1946. Actions of Radiations on Living Cells. Cambridge: University Press.

———. 1947. "The action of radiations on dilute aqueous solutions: the spatial distribution of H and OH." *Brit. Jour. Radiol. Suppl.*, No. 1, 59–64.

Mathematical Tables Project. 1940. Tables of Sine, Cosine and Exponential Integrals. Vol. I. New York: Works Progress Administration.

Moelwyn-Hughes, E. A. 1940. Physical Chemistry. Cambridge: University Press.

Opatowski, I. 1951. "Determination of the Sensitive Volume by Irradiation and the Ionization Density." *Bull. Math. Biophysics*, **13**, 263–71.

Placzek, G. 1946. The functions $E_n(x) = \int_1^\infty e^{-xu}u^{-n}du$. *Nat. Res. Counc. of Canada.* Div. Atomic Energy. Chalk River, Ontario.

Pollard, E. C. and F. Forro, Jr. 1949. "Examination of the target theory by deuteron bombardment of T — 1 phage." *Science*, **109**, 374–75.

Powell, E. O. 1943. "An integral related to the radiation integrals." *Philos. Mag.*, **34**, 600–07.

Timoféeff-Ressovsky, N. W. and K. G. Zimmer. 1947. Biophysik. Leipzig: Hirzel.

Toulis, W. J. 1950. "The decomposition of water by radiation." *U. S. Atomic Energy Commission.* UCRL–583.

Zirkle, R. E. 1935. "Biological effectiveness of α-particles as a function of ion concentration produced in their paths." *Amer. Jour. Cancer*, **23**, 558–67.

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MATHEMATICAL BIOSOCIOLOGY OF BELIEFS AND PREJUDICES

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Following a suggestion made previously (*Bull. Math. Biophysics*, **13**, 61, 1951), it is assumed that every individual has both a tendency to behave *arationally*, by accepting everything on faith, and rationally, by subjecting everything to rational analysis. Arational behavior is characterized by various beliefs, prejudices, etc., which are considered to be conditioned reactions, learned by the individual before he completely develops his faculties for rational thinking. The two tendencies are assumed to be due to excitations of two different regions of the central nervous system, and are measured by the intensities ε_f and ε_r of those excitations. Those intensities are further assumed to increase linearly with time, the increases of the two beginning, in general, at different ages. The rates of increase are considered as normally distributed in the population.The relative frequency of arational and rational behavior is determined by the difference $\phi = \varepsilon_f = \varepsilon_r$ according to equations developed previously (*Bull. Math. Biophysics*, **11**, 255, 1949).

It is shown that with the above assumptions the majority of the population, which starts with arational behavior, will, within two or three of generations, either change to rational behavior or continue indefinitely to behave arationally. This will hold as long as imitative factors are present. Expressions for the numbers of individuals who behave rationally and arationally are derived. If the intensity of conditioning toward an arational behavior decreases with increasing size of the rationally behaving minority, or, if the rationally behaving individuals are not influenced by imitation, then a slow secular trend toward rational behavior may be present. An expression is also derived for the fraction of individuals who behave rationally as a function of age. This fraction increases with increase of the age at which the beginning conditioning toward any beliefs or prejudices begins.

In this paper the attempt is made to further develop the suggestions made in a previous publication (Rashevsky, 1951b) and to derive in closed form some expressions which, in principle at least, can be verified by observation. The notations used here are somewhat different from those used in *loc. cit.*

As before (Rashevsky, 1951a,b), we consider a neural mechanism in which there are two cross-inhibited centers, one for behavior based on acceptance of everything on faith, the other for behavior based on rational analysis of everything. Each center is characterized by a level of spontaneous excitation, ε_f for the former, ε_r for the latter. The difference

$$\phi = \varepsilon_f - \varepsilon_r \tag{1}$$

determines the relative frequency of one behavior or the other, according to previously developed equations (Rashevsky, 1951a).

We again consider acceptance on faith as a conditioned process. Various beliefs, prejudices, and religious views are of the nature of conditioned reflexes. If strongly conditioned at an early age to a specific religious belief, an individual may have difficulty in abandoning this early established belief, even if he later develops critical reasoning abilities to a high degree.

Some beliefs or prejudices may be more strongly conditioned than others. Therefore, as in *loc. cit.*, we shall assume different values of ε_f for different situations.

Again, as in *loc. cit.*, we shall assume that the quantity ε_f, which measures the strength of conditioning, increases linearly with time, beginning at a certain age τ_0 at which the conditioning is started; or, if we prefer, at which the indoctrination of the belief or prejudice is begun. The rate of increase is proportional to a value ε_0, which measures the innate ability for conditioning or learning, and to a factor b, which measures the intensity of the indoctrination. Thus, if an individual is born at the time τ and the conditioning begun at the age τ_0, at any time t we have

$$\varepsilon_f = b\varepsilon_0[t - (\tau + \tau_0)]. \tag{2}$$

As to the quantity ε_r, we assume that it increases linearly with time, beginning with a certain age τ^*, so that, with λ as a constant, we have

$$\varepsilon_r = \lambda[t - (\tau + \tau^*)]. \tag{3}$$

Both the assumption of linearity and the assumption that the development of rational thinking begins at a sharply defined age τ^* are crude approximations. Subsequently we shall outline a possible generalization which will make the situation more realistic.

We shall for the time being consider the case in which

$$\tau_0 < \tau^*, \tag{4}$$

though subsequently we shall drop this restriction.

We shall write $\phi(t; \tau, \tau_0, \tau^*)$ instead of ϕ to indicate that ϕ is a function of t and of the parameters, τ, τ_0, and τ^*. When necessary, we shall use a similar notation for ε_f and ε_r.

Equations (1), (2), and (3) give, for $t \geq \tau + \tau^*$:

$$\phi(t; \tau, \tau_0, \tau^*) = b\varepsilon_0(t - \tau - \tau_0) - \lambda(t - \tau - \tau^*), \tag{5}$$

which may also be written:

$$\phi(t;\tau,\tau_0,\tau^*) = b\varepsilon_0(\tau^* - \tau_0) + (b\varepsilon_0 - \lambda)(t - \tau - \tau^*). \tag{6}$$

For $\tau + \tau_0 < t < \tau + \tau^*$ the quantity ε_r is zero, and therefore,

$$\phi = b\varepsilon_0(t - \tau - \tau_0). \tag{7}$$

Finally, for $\tau < t < \tau + \tau_0$, $\phi = 0$.

In a large population consisting of N individuals, the quantities ε_0 and λ vary from individual to individual, as does the quantity b. We shall, however, consider b as the same for all individuals, as a first approximation. As will be apparent from the subsequent developments this does not mean a loss of generality.

Consider the case in which the distribution of both ε_0 and λ is normal with corresponding means $\bar{\varepsilon}_0$ and $\bar{\lambda}$ and standard deviations σ_f and σ_r.

In a group of individuals born at τ the mean value $\bar{\phi}$ of $\phi(t;\tau,\tau_0,\tau^*)$ for $t > \tau + \tau^*$ will be [cf. eq. (6)]:

$$\bar{\phi}(t;\tau,\tau_0,\tau^*) = b\bar{\varepsilon}_0(\tau^* - \tau_0) + (b\bar{\varepsilon}_0 - \bar{\lambda})(t - \tau - \tau^*). \tag{8}$$

For $\tau + \tau_0 < t < \tau + \tau^*$ we have

$$\bar{\phi} = b\bar{\varepsilon}_0(t - \tau - \tau_0), \tag{9}$$

and for $\tau < t < \tau + \tau_0$, $\bar{\phi} = 0$.

For the standard deviation $\sigma_1(t)$ of the quantity ε_f we have for $t > \tau + \tau_0$:

$$\sigma_1(t) = b\sigma_f(t - \tau - \tau_0). \tag{10}$$

Similarly, for the standard deviation $\sigma_2(t)$ of ε_r we have for $t > \tau + \tau^*$:

$$\sigma_2(t) = \sigma_r(t - \tau - \tau^*). \tag{11}$$

For $t > \tau + \tau^*$ the standard deviation σ of ϕ is given by

$$\sigma^2(t) = \sigma_1^2(t) + \sigma_2^2(t). \tag{12}$$

Of all the individuals in the society at the time t we shall consider now only those who were born between τ and $\tau + d\tau$, or, as we shall say for brevity, those born at the time τ.

The values of ϕ of those individuals will be distributed normally, the average $\bar{\phi}$ being given by expression (8) or (9) and the standard deviation by expression (12). Let $N(\tau)d\tau$ be the number of individuals born at the time τ. Furthermore, let $f(\tau,t)$ represent the fraction of individuals born at the time τ and surviving at the time

t. Then the total number of individuals born at the time τ and still living at the time t is $N(\tau)f(\tau, t)d\tau$. Of those individuals a number

$$\frac{N(\tau)f(\tau, t)}{\sqrt{2\pi}\,\sigma(t)} \exp\left\{-\frac{[\bar{\phi}(t; \tau, \tau_0, \tau^*) - \phi]^2}{2[\sigma_1^2(t) + \sigma_2^2(t)]}\right\} d\phi \tag{13}$$

will have a ϕ between ϕ and $\phi + d\phi$.

To obtain the total number of individuals at the time t which has a ϕ between ϕ and $\phi + d\phi$ regardless of when they were born, we must integrate expression (13) with respect to τ after substituting the expressions (8), (9) (10), (11), and (12) for $\bar{\phi}(t; \tau, \tau_0, \tau^*)$, $\sigma_1(t)$, $\sigma_2(t)$, and $\sigma(t)$. The integration is to be taken from $\tau = 0$ to $\tau = t$, if $\tau = 0$ is the moment at which the social group is first formed. Since $\bar{\phi}(t; \tau, \tau_0, \tau^*)$ is not represented by a single analytical function in the whole interval $(0,t)$, we must integrate expression (13) from 0 to $t - \tau^*$, using expressions (8), (10), and (11). From $t - \tau^*$ to $t - \tau_0$ we integrate using expressions (9) and (10) and putting $\sigma_2 = 0$. Finally, in the interval $(t - \tau_0, t)$ we have $\bar{\phi} = \sigma_1 = \sigma_2 = 0$; that is, in that interval the integrand is zero.

Unfortunately the evaluation of these integrals in closed form seems to be impossible. We shall therefore use a rather crude approximation, which will not alter the essential characteristics of the relation sought or the order of magnitude of the results.

We shall assume that the distribution of ϕ at the time t for the whole population is normal with a mean value $\bar{\bar{\phi}}(t)$ of ϕ, which is equal to the *time average* of $\bar{\phi}$ in the interval $(0,t)$, and with a standard deviation $\bar{\sigma}$ which is given by

$$\bar{\sigma}^2 = \bar{\sigma}_1^2 + \bar{\sigma}_2^2, \tag{14}$$

where $\bar{\sigma}_1$ and $\bar{\sigma}_2$ are *time averages* of $\sigma_1(t)$ and $\sigma_2(t)$ in that interval.

It is more reasonable to take the time averages $\bar{\sigma}_1^2$ and $\bar{\sigma}_2^2$ of the squares, but the final expression is not changed much by this.

In computing these time averages we shall assume an exponentially increasing population, so that

$$N(\tau) = N_0 e^{\alpha t}, \tag{15}$$

and put

$$f(\tau, t) = e^{-\beta(t-\tau)}. \tag{16}$$

Remembering again that $\bar{\phi}(t, \tau, \tau_0, \tau^*)$ is given by different

expressions for $0 < t < \tau + \tau_0$; $\tau + \tau_0 < t < \tau + \tau^*$ and $t > \tau + \tau^*$, and putting

$$\alpha + \beta = \gamma, \tag{17}$$

we find

$$\bar{\bar{\phi}}(t) = \left\{ \int_0^{t-\tau^*} e^{\gamma\tau - \beta t} [b\bar{\varepsilon}_0(\tau^* - \tau_0) + (b\bar{\varepsilon}_0 - \bar{\lambda})(t - \tau - \tau^*)] d\tau \right.$$
$$\left. + \int_{t-\tau^*}^{t-\tau_0} e^{\gamma\tau - \beta t} b\bar{\varepsilon}_0 (t - \tau - \tau_0) d\tau \right\} \Big/ \int_0^t e^{\gamma\tau - \beta t} d\tau . \tag{18}$$

Evaluating the integrals, we find:

$$\bar{\bar{\phi}}(t) = \left\{ b\bar{\varepsilon}_0(\tau^* - \tau_0)(e^{\gamma(t-\tau^*)} - 1) \right.$$
$$+ \frac{b\bar{\varepsilon}_0 - \bar{\lambda}}{\gamma} \left[e^{\gamma(t-\tau^*)} - \gamma(t - \tau^*) - 1 \right] \tag{19}$$
$$\left. + \frac{b\bar{\varepsilon}_0}{\gamma} \left[e^{-\gamma\tau_0} - [1 + \gamma(\tau^* - \tau_0)] e^{-\gamma\tau^*} \right] e^{\gamma t} \right\} \Big/ \left(e^{\gamma t} - 1 \right) .$$

With increasing t the quantity $\bar{\bar{\phi}}(t)$ tends asymptotically to:

$$\bar{\bar{\phi}}_\infty = -\frac{\lambda}{\gamma} e^{-\gamma\tau^*} + \frac{b\varepsilon_0}{\gamma} e^{-\gamma\tau_0}. \tag{20}$$

If instead of considering $\tau_0 < \tau^*$, we take $\tau_0 > \tau^*$, all we have to do is to interchange τ^* and τ_0 everywhere in the preceding equations. Equations (24) and (25), and all following from them, remain unaffected by this.

If we consider plausible values for α, β, and γ to be of the order of magnitude of 10^{-2} year^{-1}, then inspection of expression (19) shows that the asymptotic value is very closely approached when $t > 1/\gamma \sim$ 100 years. Thus, if all the parameters are constant, the value of $\bar{\bar{\phi}}_\infty$, given by (20), will be reached within 2 or 3 generations and will remain constant and independent of the initial conditions at $\tau = 0$. The maximum value that $\bar{\bar{\phi}}$ could have at an early time is $b\varepsilon_0(\tau^* - \tau_0) > 0$. A bias is then present in favor of *arational* (Rashevsky, 1951a, chap. xxi) behavior, characterized by beliefs and prejudices. If

$$\lambda < b\varepsilon_0 e^{\gamma(\tau^* - \tau_0)}, \tag{21}$$

then $\bar{\bar{\phi}}_\infty$ is also positive. The bias for arational behavior persists indefinitely.

Only when

$$\lambda > b\bar{\varepsilon}_0 \, e^{\gamma(\tau^* - \tau_0)} \tag{22}$$

is $\bar{\bar{\phi}}_\infty < 0$, and the bias becomes in favor of rational behavior.

If we apply the theory of imitative behavior (Rashevsky, 1951a) to the present case, we would expect that, provided N_0 is large enough in its initial stages of development, society will exhibit predominantly arational behavior. If after a few generations a negative asymptotic $\bar{\bar{\phi}}_\infty$ is approached, society will swing into a predominantly rational behavior, provided $|\bar{\bar{\phi}}_\infty| > |\phi^*|$, where ϕ^* is the necessary threshold. This requires

$$\bar{\lambda} > \gamma \, |\phi^*| \, e^{\gamma\tau^*} + b\bar{\varepsilon}_0 \, e^{\gamma(\tau^* - \tau_0)}. \tag{23}$$

Expression (23) shows that, if the society is originally in a configuration which corresponds to arational behavior, even if $b = 0$, that is, if no prejudices are taught, it still will remain indefinitely in that configuration unless

$$\lambda > \gamma \, |\phi^*| \, e^{-\gamma\tau^*}. \tag{24}$$

We shall now proceed to find a simple expression for ϕ^*, as well as expressions for the number X and Y of individuals who behave arationally and rationally. Before doing this we might remark that by an argument similar to that which led to expression (20), we find the standard deviations $\bar{\bar{\sigma}}_1(t)$ and $\bar{\bar{\sigma}}(t)$ also tend to asymptotic values:

$$\bar{\sigma}_{1\infty} = \frac{b\,\sigma_f}{\gamma}; \quad \bar{\sigma}_{2\infty} = \frac{\sigma_r}{\gamma}. \tag{25}$$

The asymptotic value of $\bar{\sigma}$ is given by

$$\bar{\sigma}_\infty^2 = \frac{1}{\gamma^2}\,(b^2\,\sigma_f^2 + \sigma_r^2). \tag{26}$$

As has been shown previously (Rashevsky, 1951a, chap. xii), the behavioral configuration of the society is determined by the point of intersection of a certain curve and a straight line $a\psi$. It has been shown by H. G. Landau (1950) that, if the distribution function of ϕ is normal with the mean ϕ_0 and standard deviation $\bar{\sigma}$, and if the distribution of the random fluctuations in the central nervous sys-

tem (Rashevsky, 1951a) is also normal with a standard deviation s, then the curve is represented (Landau, 1950) by the function

$$2ANG\left(\frac{\psi+\phi_0}{\sqrt{s^2+\bar{\sigma}^2}}\right), \tag{27}$$

where

$$G(x) = (2\pi)^{-\frac{1}{2}} \int_0^x \exp(-x'^2/2)\,dx', \tag{28}$$

and where N denotes the total population.

As we have seen in a preceding paper (Rashevsky, 1951c), if N is very large a constant independent of N should be substituted for it into equation (27) and all the following ones. This constant will be absorbed into the constant A. The quantities X and Y, to be used subsequently, now represent the *fractions* of the total population which exhibit arational and rational behavior respectively.

The threshold value ϕ^* is that value of ϕ_0 for which the straight line $a\psi$ becomes tangent to the curve represented by the function (27) (Rashevsky, 1951a, chap. xiii). This requirement gives us the following two equations:

$$a = 2A\frac{\partial}{\partial\psi}G\left(\frac{\psi+\phi_0}{\sqrt{s^2+\bar{\sigma}^2}}\right) \tag{29}$$

and

$$a\psi = 2AG\left(\frac{\psi+\phi_0}{\sqrt{s^2+\bar{\sigma}^2}}\right). \tag{30}$$

Because of (28), equation (29) gives us

$$a = \frac{2A}{\sqrt{2\pi(s^2+\bar{\sigma}^2)}}\exp\left[-\frac{(\psi+\phi^*)^2}{s^2+\bar{\sigma}^2}\right], \tag{31}$$

which in turn leads to

$$(\psi+\phi^*) = \left\{(s^2+\bar{\sigma}^2)\log\frac{2A}{a\sqrt{2\pi(s^2+\bar{\sigma}^2)}}\right\}^{\frac{1}{2}}. \tag{32}$$

Introducing (30) into (32) we now find for the abscissa of the point of contact

$$\psi = \frac{2A}{a}G\left(\sqrt{\log\frac{2A}{a\sqrt{2\pi(s^2+\bar{\sigma}^2)}}}\right). \tag{33}$$

Introducing this expression for ψ back into (32), we find

$$\phi^* = \left\{ (s^2 + \bar{\sigma}^2) \log \frac{2A}{a\sqrt{2\pi(s^2 + \bar{\sigma}^2)}} \right\}^{\frac{1}{2}} - \frac{2A}{a} G\left(\left\{ \log \frac{2A}{a\sqrt{2\pi(s^2 + \bar{\sigma}^2)}} \right\}^{\frac{1}{2}} \right). \tag{34}$$

As A increases G tends to unity, while the absolute value of the first term of the right side increases indefinitely. Therefore ϕ^* increases indefinitely with A, as $\sqrt{\log A}$. With increasing s or $\bar{\sigma}$ the first term of the right side again increases, while G tends to -1. Thus, on the positive branch where ϕ^* is negative, it goes to $-\infty$ as either s or $\bar{\sigma}$ increases indefinitely.

Introducing expression (34) into inequality (23), we obtain the condition that a society would *within a couple of generations* adopt a preponderantly rational behavior. Since none of the known societies behave preponderantly rationally, because superstitions, religious creeds, and prejudices of various kinds are still characteristic of the majority, we may draw the conclusion that inequality (23) is never satisfied.

We shall now derive an expression for the fraction X of individuals who exhibit arational behavior after society has approached the stationary state which is characterized by the values given by expressions (20) and (26). To do this we must solve equation (30) for ψ when $\phi_0 = \bar{\bar{\phi}}_\infty$ and $\bar{\sigma} = \bar{\sigma}_\infty$. Since the $G(x)$ function is similar in its general behavior to the function $1 - e^{-x}$, we may use the method of successive approximations suggested previously (Rashevsky, 1951a, pp. 91–2). We shall consider the case in which a is sufficiently small and therefore X is close to unity, and we shall use only the first approximation, which is obtained by putting $\psi = A/a$ in the right side of (30). Thus

$$\psi^* = \frac{2A}{a} G\left(\frac{A + a\bar{\bar{\phi}}_\infty}{a\sqrt{s^2 + \bar{\sigma}_\infty^2}} \right). \tag{35}$$

If Y is the fraction of individuals who exhibit rational behavior, then (Rashevsky, 1951a, chap. xiii) we have

$$X + Y = 1 \tag{36}$$

and

$$X - Y = \frac{a\psi^*}{A}. \tag{37}$$

Equations (36) and (37), together with (35), give

$$X = \frac{1}{2}\left[1 + 2G\left(\frac{A + a\bar{\bar{\phi}}_\infty}{a\sqrt{s^2 + \bar{\sigma}_\infty^2}}\right)\right] \tag{38}$$

and

$$Y = \frac{1}{2}\left[1 - 2G\left(\frac{A + a\bar{\bar{\phi}}_\infty}{a\sqrt{s^2 + \bar{\sigma}_\infty^2}}\right)\right]. \tag{39}$$

As $\bar{\bar{\phi}}_\infty$ tends to $+\infty$, $X \to 1$, $Y \to 0$. As $A \to \infty$ we also have $X \to 1$.

Since both $\bar{\bar{\phi}}_\infty$ and $\bar{\sigma}_\infty$ are approached within a rather short time (of the order of one generation) after a few generations, regardless of the initial condition, the fractions X and Y become practically constant. If $\bar{\bar{\phi}}_\infty$ is either positive or not sufficiently negative, then, if arational behavior has been adopted initially by the society as a whole, it will persist indefinitely, unless inequality (23) is satisfied, which, as we have just concluded, is not likely.

The situation, however, becomes different if we take into account possible variations of b, which measures the intensity of indoctrination with a given belief or prejudice. This intensity may be considered on the average as being the smaller, the larger Y, the relative number of individuals who behave rationally. Any individual is exposed at the age τ_0 both to the effects of the fraction X of arationally behaving individuals and the fraction Y of rationally behaving ones. It is true that some individuals, born in an arationally behaving family, may be more shielded from the rationally behaving individuals than others. But on the average it is a fair approximation to put

$$b = b_0(1 - Y), \tag{40}$$

where b_0 is a constant.

Now let $\lambda > b\varepsilon_0$, so that in the course of the first few generations $\bar{\bar{\phi}}(t)$, while remaining positive, decreases. This decrease in $\bar{\bar{\phi}}(t)$ will result in an increase of Y. Such an increase in Y will result in a decrease of b, and therefore in an increase of $\lambda - b\varepsilon_0$, and hence in a more rapid decrease of $\bar{\bar{\phi}}$. This further enhances the increase of Y. We shall now investigate whether under those conditions society will eventually adopt a preponderantly rational behavior.

This process of decrease of b is a very slow one, at least when Y is very small as is the case in initial stages. An appreciable change in b is to be expected only after a time which is much larger than $1/\gamma$. Since $\bar{\sigma}$ approaches its asymptotic value $\bar{\sigma}_\infty$ approximately within the time $1/\gamma$, in our subsequent argument we may consider that the value $\bar{\sigma}_\infty$ has been reached and remains constant. If the change is very slow, so that b does not vary much during the time $t_1 = 1/\gamma$, we may consider the whole situation as a succession of stationary states, and $\bar{\bar{\phi}}_\infty$ as a slowly varying function of time.

The precise formulation of the above idea leads to rather hopeless looking functional equations. The following approximate treatment gives us, however, an answer to our question. We have from (40), (39), and (28)

$$\begin{aligned} \frac{db}{dt} &= -b_0 \frac{dY}{dt} \\ &= \left\{ \frac{1}{\sqrt{2\pi(s^2+\bar{\sigma}_\infty^2)}} \exp\left[-\frac{[A + a\bar{\bar{\phi}}_\infty]^2}{2a^2(s^2+\bar{\sigma}_\infty^2)} \right] \right\} \frac{d\bar{\bar{\phi}}_\infty}{dt}. \end{aligned} \tag{41}$$

The asymptotic value given by expression (20) is approached approximately after a time $1/\gamma$. As we have seen, the initial value of $\bar{\bar{\phi}}(t)$ is approximately $b\bar{\varepsilon}_0(\tau^* - \tau_0)$; the asymptotic value is given by (20). If we assume τ^* and τ_0 to be of the order of magnitude of a few years, then, because $\gamma \sim 10^{-2}$ year^{-1}, we can expand the exponentials in expression (20), retaining only the linear terms. We then find that if (22) is satisfied the increment of $\bar{\bar{\phi}}(t)$ during the time $1/\gamma$ is approximately $-(\lambda - b\varepsilon_0)/\gamma$. Hence roughly the order of magnitude of $d\bar{\bar{\phi}}(t)/dt$ is

$$\frac{d\bar{\bar{\phi}}_\infty}{dt} \sim -\frac{\beta(\lambda - b\,\varepsilon_0)}{\gamma} < 0. \tag{42}$$

Introducting this into expression (41) we obtain:

$$\begin{aligned} \frac{db}{dt} = -\frac{\beta(\lambda - b\,\bar{\varepsilon}_0)}{\gamma} \frac{1}{\sqrt{2\pi(s^2+\bar{\sigma}_\infty^2)}} \times \\ \exp\left[-\frac{[A + a\bar{\bar{\phi}}_\infty]^2}{2a^2(s^2+\sigma_\infty^2)} \right], \end{aligned} \tag{43}$$

which shows that b does decrease eventually to zero.

In equation (43) $\bar{\bar{\phi}}_\infty$ is itself a function of b, according to equation (20). As b decreases, $\bar{\bar{\phi}}_\infty$ tends to a negative value $-\frac{\lambda}{\gamma} e^{-\gamma\tau^*}$. For sufficiently small values of b, when the asymptotic value is almost reached, the exponential term in equation (43) remains practically constant. In that case equation (43) becomes of the form

$$\frac{db}{dt} = -K(\lambda - b\,\bar{\varepsilon}_0)\,. \tag{44}$$

Integrated with the initial condition $b = b_0$ at $t = 0$, this gives

$$b = \frac{1}{\bar{\varepsilon}_0}\left[\lambda - (\lambda - b_0\bar{\varepsilon}_0)\, e^{k\bar{\varepsilon}_0 t}\right]. \tag{45}$$

According to this equation, b becomes equal to zero for

$$t = \frac{1}{k\,\bar{\varepsilon}_0} \log \frac{\gamma}{x - b_0\,\bar{\varepsilon}_0}. \tag{46}$$

If condition (24) is satisfied, then sometime before the time given by (46), the society will change to a rational behavior.

A secular trend toward a change to a preponderantly rational behavior may be obtained, however, if we consider the possibility that an individual who chooses rational behavior also becomes free from imitative influnces, a situation which is psychologically plausible. In that case the offspring of the fraction Y of individuals will have a zero b and will not be subject to imitation. Then the situation will be described by equation (24) [cf. *loc. cit.*] into which we now introduce α for β, and use Y, as given by equation (39), for α. In our present notation equation (25) of *loc. cit.* reads

$$\frac{n_1}{N} = 1 - e^{\alpha Y t}, \tag{47}$$

where n_1 is the total progeny of the rationally behaving fraction of the population, as distinguished from Y, which is the fraction of individuals born of the arationally behaving majority but which adopts rational behavior with age.

The above conclusions hold, however, only for the case of imitative behavior. If each individual acts quite independently, the situation is different. With sufficiently small values of

a, σ_f and σ_r, a relatively small positive value of $\bar{\bar{\phi}}(t)$—say, the initial value of $b\,\bar{\varepsilon}_0(\tau^* - \tau_0)$—may result in the vast majority of the population choosing arational behavior. If $\bar{\bar{\phi}}_\infty$ is still sufficiently positive, then most of the population will still exhibit an arational behavior after the asymptotic state is approached. However, the quantities X and Y now vary continuously with $\bar{\bar{\phi}}_\infty$. We now have

$$X = \tfrac{1}{2}\left[1 + 2G\left(\frac{\bar{\bar{\phi}}_\infty}{\sqrt{s^2 + \bar{\sigma}_\infty^2}}\right)\right]; \tag{48}$$

$$Y = \tfrac{1}{2}\left[1 - 2G\left(\frac{\bar{\bar{\varphi}}_\infty}{\sqrt{s^2 + \bar{\sigma}_\infty^2}}\right)\right]. \tag{49}$$

If we now make the assumption expressed by equation (40) and repeat the argument following that equation, we find, instead of (43):

$$\frac{db}{dt} = -\frac{\beta(\bar{\lambda} - b\,\bar{\varepsilon}_0)}{\gamma^2}\,\frac{1}{\sqrt{2\pi(s^2 + \bar{\sigma}_\infty^2)}}\exp\frac{\bar{\bar{\phi}}}{2(s^2 + \bar{\sigma}_\infty^2)}. \tag{50}$$

Again b decreases to zero. From equation (20) we see that eventually $\bar{\bar{\phi}}_\infty$ becomes equal to $-(\lambda/\gamma)e^{-\gamma\tau^*}$, which is negative. The majority will exhibit rational behavior.

As a last problem we shall consider the following one. Consider at a time t all individuals with an age between θ and $\theta + d\theta$, with $\theta > \tau^*$. For all these individuals ϕ will be distributed normally and the mean value will be given by equation (8) in which we put $t - \tau = 0$. Hence it will be given by

$$\bar{\phi} = b\,\bar{\varepsilon}_0(\tau^* - \tau_0) - (b\,\bar{\varepsilon}_0 - \bar{\lambda})(\theta - \tau^*). \tag{51}$$

The standard deviation, according to equations (10), (11), and (12), is given by

$$\sigma = \sqrt{b^2\sigma_f^2(\theta - \tau_0)^2 + \sigma_r^2(\theta - \tau^*)^2}. \tag{52}$$

If there is no imitation in the group, then the fraction Y of individuals who at the age θ behave rationally is given by

$$Y = \tfrac{1}{2}\left[1 - 2G\left(\frac{b\,\bar{\varepsilon}_0(\tau^* - \tau_0) + (b\,\bar{\varepsilon}_0 - \bar{\lambda})(\theta - \tau^*)}{\sqrt{s^2 + b^2\sigma_f^2(\theta - \tau_0)^2 + \sigma_r^2(\theta - \tau^*)}}\right)\right]. \tag{53}$$

In case of imitative behavior, the value of ϕ for each individual is increased by the amount ψ^* given by expression (35) (Rashevsky 1951a, chap. xiii). Hence $\bar{\phi}$ is increased by the same amount. That amount is determined by the dynamics of the whole population of N individuals of all ages, of which we now consider a subset of age θ. Hence

$$Y = \tfrac{1}{2}\left[1 - 2G\left(\frac{\psi^* + b\,\bar{\varepsilon}_0(\tau^* - \tau_0) + (b\,\bar{\varepsilon}_0 - \bar{\lambda})(\theta - \tau^*)}{\sqrt{s^2 + b^2\sigma_f^2(\theta - \tau_0)^2 + \sigma_r^2(\theta - \tau^*)}}\right)\right]. \quad (54)$$

Equations (53) and (54) give us, for the two cases, expressions which can be verified by sociological observation. The particular type of arational behavior may be, for example, religious creed. Then Y gives the percentage of agnostics at the age θ as a function of other observable quantities.

If $\bar{\lambda} > b\,\bar{\varepsilon}_0$, then Y increases with θ. The smaller τ_0 for a fixed τ^*, that is, the earlier religious education begins, the smaller Y at a given age θ, according to equation (53). The same follows from equations (54) and (35).

As we said at the beginning, the assumption of a linear increase in ε_f and ε_r is not very realistic. More likely both quantities reach a saturation value and may be better approximated by

$$\varepsilon_f = K_f(1 - e^{-k_f t})\,; \quad \varepsilon_r = K_r(1 - e^{-k_r t})\,; \quad (55)$$

where the parameters K_f, k_f, K_r, and k_r are distributed normally or otherwise. If the distribution of those parameters is known, the derivation of the distribution of $\varepsilon_f - \varepsilon_r$ with t as a parameter is straightforward but leads to computational difficulties and does not lead readily to closed expressions. This problem should, however, be considered as the next step.

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LITERATURE

Rashevsky, N. 1951a. *Mathematical Biology of Social Behavior.* Chicago: The University of Chicago Press.

——— 1951b. "Outline of a Mathematical Biosociology of Beliefs and Prejudices." *Bull. Math. Biophysics,* **13**, 61–8.

——— 1951c. "Note on Imitative Behavior and Information." *Ibid.*, 147–51.

Landau, H. G. 1950. "A Note on the Effect of Imitation in Social Behavior." *Bull. Math. Biophysics,* **12**, 221–35.

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THE KINETICS OF INVERTASE ACTION*

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A method of obtaining better fits to experimental curves for the hydrolysis of sucrose in the presence of invertase is found by assuming that the reaction is first-order, but that there is an initial time delay before this form is assumed. More rigorously, a system of two differential equations describing the reaction is established, assuming that the formation of enzyme-substrate complex is irreversible, and a solution is obtained relating, at any time, the concentration of the products, the total concentration of complex which has been formed in that time, and the time. This solution is compared with other equations for the reaction and is used to calculate reaction constants. Curves showing the concentration of complex existing at time t are given and are employed in calculating an "equivalent" enzyme concentration. This expression is discussed.

There have been many attempts to analyze the kinetics of the action of invertase on sucrose. The earlier work has been summarized by R. Kuhn (1925) and J. B. S. Haldane (1930). These analyses are based mainly on the theories of L. Michaelis and M. L. Menten (1913), although several empirical formulations have also been made. H. Lineweaver and D. Burk (1934) have used this earlier development in their determinations of dissociation constants by their reciprocal methods. Some recent discussions of the kinetics of enzyme reactions are given by P. W. Wilson (1949), A. E. Stearn (1949), J. B. Sumner and K. Myrbäck (1950) and E. A. Moelwyn-Hughes (1950).

During the course of experiments on the effects of mercurials on invertase activity by C. L. Gemmill and E. M. Bowman (1950), considerable data was obtained which lent itself to mathematical analysis. This analysis will be divided into three phases: (1) determination of the over-all reaction velocity; (2) determination of the velocity of the enzyme-substrate reaction; and (3) a method of calculation of equivalent enzyme concentration.

Determination of Over-all Reaction Velocity. It is generally held

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that the hydrolysis of sucrose in the presence of invertase proceeds in accordance with the Michaelis-Menten equation. However, it is still considered (Sumner and Myrbäck, 1950, p. 26) valid to use first order equations to calculate an over-all velocity constant for reactions which approximate closely to monomolecular reactions. That is, for the sucrose-invertase reaction, if y is the concentration of products at time t, and if S_0 is the initial concentration of sucrose, then

$$\frac{dy}{dt} = K(S_0 - y), \tag{1}$$

from which we obtain:

$$y = S_0(1 - e^{-Kt}), \quad \text{or} \quad K = \frac{1}{t} \ln \frac{S_0}{S_0 - y}. \tag{2}$$

This function of time gives a curve which does not fit the curve obtained by experiment, as indicated in Figure 1. Further, for K

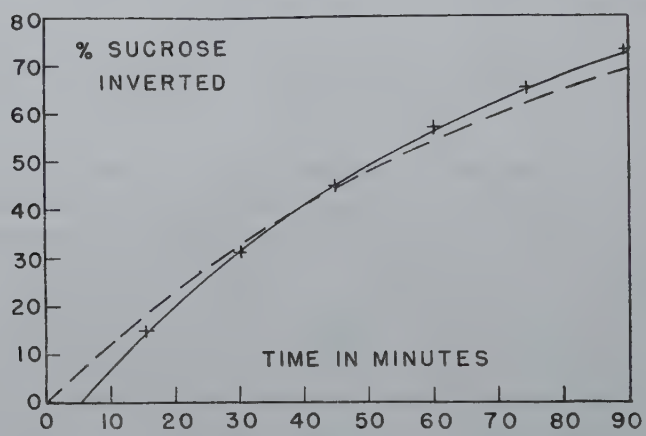

FIGURE 1. Comparison of monomolecular curve (dotted line) with curve constructed using the θ assumption (solid line) for a sucrose-invertase experiment with $S_0 = 12$ per cent. Ordinates, per cent sucrose inverted. Abscissae, time in minutes. $K = .0146$, $\theta = 4.2$ mins.

taken as the mean of the values calculated using expression (2), it was observed that the theoretical curve crossed the experimental curve in all cases, being above the latter initially. If the experimental curve were exponential, with S_0 as its upper bound, this would occur only for $t = 0$.

For these reasons a time lag of θ minutes from $t = 0$ to $t = \theta$ was assumed to occur before the reaction assumed the exponential

form. With this assumption, better fits to the experimental data were obtained, as indicated in Figure 1 for one experiment. This assumption takes mathematical form as a change in the limits of integration of (1). Thus, for $t \geq \theta$,

$$K \int_{t=\theta}^{t=t} dt = \int_{0}^{y} \frac{dy}{S_0 - y}, \quad \text{or} \quad K(t-\theta) = \ln \frac{S_0}{S_0 - y}; \tag{3}$$

while, for $0 \leq t < \theta$, $y = 0$.

Expression (3), which is linear in the variables t and

$$\ln(S_0/S_0 - y),$$

is in convenient form for application of the method of least squares to calculate the numbers K and θ. The results of such calculations for a series of eight experiments are given in Table I.

TABLE I

CALCULATIONS OF K AND θ BY MEANS OF EXPRESSION (3); DATA OF GEMMILL AND BOWMAN (1950)

S_0	*ENZYME*	*DRUG*	*TEMP.*	K (Min.$^{-1}$)	θ (min.)
3%	Invertase	None	29.7°C.	.0508	3.1
6%	Invertase	None	29.7°C.	.0318	2.6
12%	Invertase	None	29.7°C.	.0146	4.2
6%	Invertase	Ascorbic Acid	29.7°C.	.0227	0.7
6%	Invertase	$HgCl_2$	29.7°C.	.0128	2.7
6%	Invertase	None	21.1°C.	.0207	4.0
6%	Invertase	$HgCl_2$	21.1°C.	.0093	5.8
6%	Invertase	$HgCl_2$	21.1°C.	.0090	4.5

The introduction of the time θ in the equation has the practical value of obtaining a better fit of the curve to the experimental points. It has the theoretical value of showing that there is a finite time after the substrate is in contact with the enzyme before a measurable increase is observed in the reaction products. It also gives additional evidence for the pseudo-monomolecular type of reaction taking place in this case.

Determination of Velocity of Enzyme-Substrate Reaction. The observation that the assumption of a time lag gave better fits to experimental curves is an empirical method. However, it is of such a nature as to indicate that the appearance of the products begins with zero velocity. First order reactions following equation (2) begin

with a velocity equal to KS_0, which is not zero. Hence, further analysis was made of the action of this process.

The assumptions used subsequently are:

1. The reaction is described, as usual, by

$$E + S \rightleftarrows ES \rightarrow E + P.$$

The rate of formation, at any time t, of the products, P, is proportional to the concentration of the intermediate complex, ES, at that time, and the rate of production of ES is proportional to the product of the concentrations of E and of S.

2. The velocity constant for the reverse reaction, $ES \rightarrow E + S$, is negligible compared to that of the direct reaction.

3. There is no inhibition by the products of the reaction.

4. The enzyme regenerated is all active.

Let x be the total concentration of ES which has formed in time t, and let y be the total concentration of products formed in time t. Because of assumptions 2, 3, and 4, we have that at time t, $x - y$ is the concentration of ES, $E_0 - (x - y)$ is the concentration of free enzyme, and $S_0 - x$ is the concentration of substrate. Then, using assumption 1, the equations describing the course of the reactions are:

$$\frac{dy}{dt} = K_1(x - y) \tag{4}$$

and

$$\frac{dx}{dt} = K_2(E_0 - x + y)(S_0 - x). \tag{5}$$

The equation for the overall reaction would be obtained by integrating these equations simultaneously. This has not been completely done. However, the single equation resulting from these by the substitution, $y - S_0 = z$, is

$$z'' + (a - bz)z' - cz'^2 + dz = 0, \tag{6}$$

where $a = K_1 + K_2E_0$, $b = K_2$, $c = K_2/K_1$, and $d = K_1K_2E_0$.

By the usual substitutions, $p = z'$ and $p(dp/dt) = z''$, equation (6) becomes

$$p\frac{dp}{dt} + (a - bz)p - cp^2 + dz = 0, \tag{7}$$

which is a form of Abel's equation (Sylow and Lie, 1881) for which no solution in terms of elementary or tabulated functions has yet been given.

A solution, $y = f(x, t)$, is easily obtained, however. Into equation (5) we substitute $x - y = (1/K_1)(dy/dt)$, from equation (4). This gives us

$$\frac{1}{K_2(S_0 - x)}\frac{dx}{dt} = E_0 - \frac{1}{K_1}\frac{dy}{dt},$$

which is directly integrable. Using the initial conditions $x(0) = 0$ and $y(0) = 0$, we obtain

$$\frac{1}{K_2}\ln\frac{S_0}{S_0 - x} = E_0 t - \frac{1}{K_1}y,$$

or

$$y = K_1 E_0 t - \frac{K_1}{K_2}\ln\frac{S_0}{S_0 - x}. \tag{8}$$

This expression demonstrates the relation existing between the quantities x and y, but does not give the actual curve y as a function of t. Interesting results may be obtained, though, by the application of this equation to experimental results, as will be shown in a later paragraph.

The term $K_1 E_0 t$ in equation (8) might create the impression that enzymatic reactions approximating the assumptions made here are initially of zero order; i.e., that at the beginning of the reaction the production of y proceeds linearly. However, the initial slope of the function $y(t)$ is necessarily zero, since, by assumption,

$$\frac{dy}{dt} = K_1(x - y) \tag{4}$$

and $x(0) - y(0) = 0$.

From the above point of view, an assumption that sucrose inversion under the action of invertase is a monomolecular reaction is equivalent to an assumption that $x(t)$ represents the total concentration of *products* formed in time t and that $y(t)$ is identically zero throughout the reaction. Under these circumstances, the solution (8) becomes

$$0 = K_1 E_0 t - \frac{K_1}{K_2}\ln\frac{S_0}{S_0 - x},$$

or

$$x = S_0(1 - e^{-K_2E_0t}), \tag{9}$$

which is the ordinary monomolecular expression with $K = K_2E_0$. This fact explains the observation that K, as calculated from the monomolecular expression, is proportional to the initial enzyme concentration.

The time-action function given by G. E. Cullen and D. D. Van Slyke (1914) (and Van Slyke, 1942) is

$$t = \frac{1}{K_C} \ln \frac{a}{a - x} + \frac{x}{K_D}, \tag{10}$$

where K_C is the reaction constant for formation of the enzyme-substrate complex, K_D is the reaction constant for the hydrolysis, and x is the total concentration of the products. In the notation used here, this becomes

$$t = \frac{1}{K_2} \ln \frac{S_0}{S_0 - y} + \frac{y}{K_1},$$

or

$$y = K_1t - \frac{K_1}{K_2} \ln \frac{S_0}{S_0 - y}. \tag{11}$$

This equation, except for the coefficient of t, is what the solution (8) becomes for large t, since then x is approximately equal to y, the concentration of ES existing at time t approaching zero as t increases. In that case, (8) becomes (for large t)

$$y = K_1E_0t - \frac{K_1}{K_2} \ln \frac{S_0}{S_0 - y}. \tag{12}$$

The discrepancy is accounted for by examination of the development of formula (10). If K_C and K_D are the quantities stated above, then K_C must have units of (moles^{-1} $\times$ min.$^{-1}$) and K_D must have units of (min.$^{-1}$). Then the "time required for one cycle," $(1/K_CS) + (1/K_d)$, which occurs in the Cullen and Van Slyke development, is in units of time, whereas it should be in units of time per mole, or equivalent mole (see below), of enzyme. This is indicated more clearly in their equation,

$$-\frac{dS}{dt} = \frac{1}{(1/K_CS) + (1/K_D)},$$

in which the left side has units of moles per unit time and the right side has units of reciprocal time. Hence, it is seen that their K_C is our K_2E_0 and their K_D is our K_1E_0. Therefore, in our notation, equation (10) is really

$$y = K_1E_0t - \frac{K_1}{K_2}\ln\frac{S_0}{S_0 - y},$$

which is the same as equation (12).

Since equation (12) is valid for large t, it may be used to determine the values K_1E_0 and K_1/K_2, by substituting into the expression experimental values for y. For large t, though, experimental errors are more significant, since then the time-action curve has become flat. Therefore, care must be observed in the application of equation (12).

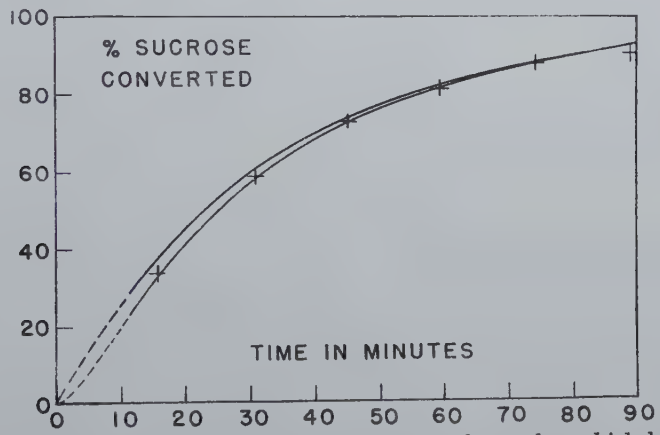

FIGURE 2. Upper curve: total concentration, x, of complex which has formed in time t. Lower curve: concentration of products at time t. Ordinates, per cent sucrose converted. Abscissae, time in minutes.

As an example, using the experimental results obtained in the experiment whose graph is given in Figure 1, the following evaluations were made:

$$K_1E_0 = .0105 \text{ (moles/min.)}, \quad \frac{K_1}{K_2} = .547 \text{ (moles)},$$

and

$$K_2E_0 = \frac{K_1E_0}{K_1/K_2} = .0192 \text{ (min.}^{-1}\text{)}.$$

The solution (8) may be written

$$x = S_0(1 - e^{-K_2(E_0t - y/K_1)}). \tag{13}$$

Using the constants calculated above and the experimentally obtained values for y, this function gives the total concentration of the complex ES which has been formed in time t. The curve thus obtained resembles more closely the curves previously thought to represent the time-action curve for the formation of products of the reaction. Figure 2, using y values from the approximating curve obtained by the method of part (1), shows how the x-curve compares with the y-curve in another experiment.

A second method of obtaining values for the constants is possible. Since the assumption of a time lag, θ, gave curves which fitted the data accurately, it may be assumed that the expression (2) represents the experimental curve for large t. The expression (12), rewritten, becomes

$$y = S_0(1 - e^{-K_2(E_0t - y/K_1)}),$$

which is also valid for large t. Hence, the exponents must be approximately equal, or

$$K_2E_0t - \frac{K_2}{K_1}y = K(t - \theta).$$

This is a linear expression,

$$y = \frac{K_1}{K_2}(K_2E_0 - K)t - \frac{K_1K}{K_2}\theta.$$

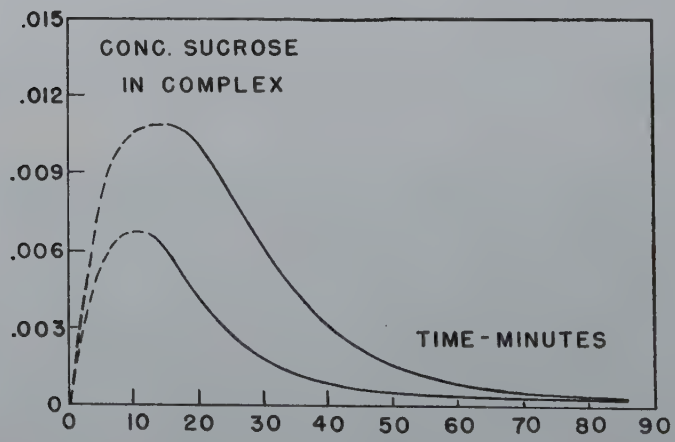

FIGURE 3. Concentration, $x - y$, of sucrose in the complex at time t. Upper curve: $S_0 = 12$ per cent. Lower curve: $S_0 = 6$ per cent. Ordinates, concentration of sucrose in complex. Abscissae, time in minutes.

But for large t, the curve is flat, $dy/dt = 0$, or $K_2E_0 = K$. Therefore, if K is accurately calculated in an experiment which is carried over a long period of time, it has approximately the value K_2E_0.

For the experiment whose graph is Figure 2, this method gives $K_2E_0 = K = .0318$. This experiment, with $S_0 = .1512\ M$, was carried out long enough for $y(t)$ to level off. Hence the data at three large values of t were used in the expression (12) to obtain an average value $K_1/K_2 = .576$.

In Figure 3, the curve $x - y$, representing the concentration of sucrose existing in the complex ES at time t, has been plotted for the two experiments above, using the curves of part (1) as the experimental y-curve. B. Chance (1943) devised a method for direct observation of the curve $x - y$ for the peroxidase-H_2O_2-reaction. The curves obtained by the methods described above show an obvious similarity with respect to shape to those reported by Chance. In the same article, the G. E. Briggs and Haldane (1925) equations, which are similar to those given here, have been integrated by means of a differential analyzer, without the assumption made by them that $d(x - y)/dt$ is always so small that it may be considered to be zero throughout the reaction.

Method of Calculation of Equivalent Concentration of Enzyme. Using values obtained for $x - y$, as a function of t, the value of K_1 may be calculated according to equation (4). The slopes, dy/dt, must be obtained from the graph of y as a function of t. Assuming a constant error of observation, the following values were found in the two experiments whose graphs are given in Figures 1 and 2. In the first, $K_1 = .2165$ (min.$^{-1}$) and, since $K_1E_0 = .0183$, we have $E_0 = .0479\ M$

If the molecular weight of invertase is around 50,000 this value of E_0 leads to an unreasonably high density for the invertase preparation used in these experiments. Therefore this figure cannot represent the *actual* initial concentration of the enzyme. It may, however, represent an *equivalent* concentration in the sense that, if one molecule of enzyme combined with a large number, n, of substrate molecules, rather than as postulated in part 2, then the number found above would represent n times the *actual* initial concentration of invertase. To obtain the actual initial enzyme concentration knowledge of the magnitude of n is required.

It may be that before any of the ES complex is hydrolyzed a certain fixed number, n, of substrate molecules must combine with an enzyme molecule. In that case, one would expect an actual time delay as postulated in part (1). It is much more likely that the number n is a statistical figure, namely, the average number of molecules

of substrate which are associated with one molecule of enzyme in the complex. In the latter case, one would probably expect the initial zero velocity as developed in part (2).

LITERATURE

Briggs, G. E. and J. B. S. Haldane. 1925. "A Note on the Kinetics of Enzyme Action." *Biochem. Jour.*, **19**, 338–39.

Chance, B. 1943. "The Kinetics of the Enzyme-Substrate Compound of Peroxidase." *Jour. Biol. Chem.*, **151**, 553–77.

Gemmill, C. L. and E. M. Bowman. 1950. "The Effects of Mercurial Compounds on Invertase." *Jour. Pharm. & Exp. Ther.*, **100**, 244–49.

Haldane, J. B. S. 1930. *Enzymes.* London: Longmans, Green & Co.

Kuhn, R. 1925. "Physikalische Chemie der Fermente." *Tabulae Biologicae*, **2**, 25–50.

Lineweaver, H. and D. Burk. 1934. "The Determination of Enzyme Dissociation Constants." *Jour. Amer. Chem. Soc.*, **56**, 658–66.

Michaelis L. and M. L. Menten. 1913. "Die Kinetik der Invertinwirkung." *Biochem. Z.*, **49**, 333–69.

Moelwyn-Hughes, E. A. 1950. "Physical Chemistry and Chemical Kinetics of Enzymes." *The Enzymes*, vol. 1, part 1, (Ed. J. B. Sumner and K. Myrbäck). New York: Academic Press, Inc. 28–78.

Stearn, A. E. 1949. "Kinetics of Biological Reactions with Special Reference to Enzymic Processes." *Adv. Enzymology*, **9**, 25–74.

Sumner, J. B. and K. Myrbäck. 1950. "Introduction." *The Enzymes*, vol. 1, part 1, (Ed. J. B. Sumner and K. Myrbäck). New York: Academic Press, Inc., 1–27.

Sylow, L. and S. Lie. 1881. *Oeuvres de Niels Henrik Abel*, vol. II. Christiania, Norway: Grondahl and Son.

Van Slyke, D. D. and G. E. Cullen. 1914. "The Mode of Action of Urease and of Enzymes in General." *Jour. Biol. Chem.*, **19**, 141–80.

Van Slyke, D. D. 1942. "The Kinetics of Hydrolytic Enzymes and their Bearing on Methods for Measuring Enzyme Activity." *Adv. Enzymology*, **2**, 33–47.

Wilson, P. W. 1949. "Kinetics and Mechanisms of Enzyme Reactions." *Respiratory Enzymes*, (Ed. H. A. Lardy). Minneapolis: Burgess Publishing Co., 16–57.

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THE GAME OF "GOSSIP" ANALYZED BY THE THEORY OF INFORMATION

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This paper deals with an analysis of a distributed model of the game of "gossip," in which a message is passed through a line of individuals, and the final (in general, garbled) result is compared with the original ungarbled message. The deterioration of information (defined in the sense of Shannon and Wiener) along the line is calculated, and exact as well as asymptotic formulas suggesting approximate linear electric network analogues are obtained.

I. *Object of this Paper.* In discussing communication nets involving human beings and/or other automata one is tempted to call upon analogies from the theory of linear electric networks to describe the mutual exchange of information in terms of analogous current or voltage propagation. In this paper we consider a particular type of communication system, and investigate the approximations under which for that particular case an analogy can rigorously be drawn, using the strict definition of information proposed by Shannon and Wiener.*

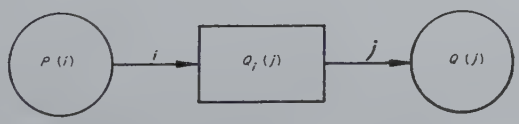

FIGURE 1. Fundamental Communication system.

II. *The Theory of Information.* Consider a communication system (Fig. 1) described by the square $n \times n$ matrix

$$P(i, j) = \text{joint probability that the } i\text{th symbol is sent, and, as a result of this, the } j\text{th symbol received.} \tag{1}$$

We shall define

*See list of references at end of paper.

$$P(i) = \sum_{j=1}^{n} P(i, j) = \text{a priori probability of sending symbol } i, \tag{2}$$

$$Q(j) = \sum_{i=1}^{n} P(i, j) = \text{a priori probability of receiving symbol } j, \tag{3}$$

$$Q_i(j) = P(i, j)/P(i) = \text{conditional probability that } j \text{ is received if } i \text{ is sent.} \tag{4}$$

It is evidently necessary that

$$\sum_j Q_i(j) = 1, \ (i = 1, 2, \cdots, n). \tag{5}$$

Shannon has shown* that the information rate of the communication system of Figure 1 should be defined as

$$R = H - E, \tag{6}$$

where

$$H = -\sum_{j=1}^{n} Q(j) \log Q(j) \text{ is the negentropy of the received symbols}\dagger \tag{7}$$

$$E = -\sum_{i,j=1}^{n} P(i, j) \log Q_i(j) \text{ is the equivocation of the system} \tag{8}$$

In the special case when all the symbols to be sent are equally likely we have

$$P(i) = 1/n. \tag{9}$$

Therefore, $P(i, j) = (1/n) Q_i(j)$, giving

$$E = -(1/n) \sum_{i,j,=1}^{n} Q_i(j) \log Q_i(j). \tag{10}$$

Also, if in addition, $Q_i(j) = Q_j(i)$

$$Q(j) = \sum_{i=1}^{n} P(i) Q_i(j) = (1/n) \sum_{j=1}^{n} Q_i(j) = (1/n) \tag{11}$$

according to (5).

*Cf. Shannon, 1948a, p. 409; also see Reich, 1951 for a discussion of the arbitrariness of the choice of the definition of information. Shannon uses $H(y)$ for our H, and $H_x(y)$ for our E. Shannon uses logs to the base 2; we employ natural logs.

†The term "negentropy" is due to Brillouin, 1950.

In this particular case, therefore, $H = \log n$, so that

$$R = \log n + (1/n) \sum_{i,j=1}^{n} Q_i(j) \log Q_i(j). \tag{12}$$

III. *Model for the Game of Gossip.* The game is postulated to consist in selecting a symbol (message) at random from a set of n symbols, such that all n symbols are a priori equally likely, and propagating it down the line of individuals. The participants are assumed to know what the a priori possible messages are, and to realize that they are a priori equally likely.

We shall let x measure distance from the beginning, or origin of the line.

We now make the idealizing postulate that if the symbol arriving at x is the ith symbol, then the probability that an arbitrary symbol j arrives at $x + dx$ is given by the conditional probability matrix

$$[Q_i(j)_{x,x+dx}] = \begin{bmatrix} 1-\alpha(n-1)dx & \alpha dx & \cdots & \alpha dx \\ \alpha dx & 1-\alpha(n-1)dx & \cdots & \alpha dx \\ \cdots & \cdots & \cdots & \cdots \\ \alpha dx & \alpha dx & & 1-\alpha(n-1)dx \end{bmatrix}.$$

Here α should be thought of as a number proportional to the density of human beings per unit distance along the line. In the realistic case distance would be measured as proportional to the number of human beings. Therefore α plays the role of a characteristic frailty (independent of n) which must be found by experiment.*

Symbolically

$$Q_i(j)_{x,x+dx} = (1 - \alpha n dx)\, \delta_{ij} + \alpha dx\dagger. \tag{13}$$

We shall let

$$f_{ij}(x) = \text{conditional probability that } j \text{ will be received at } x \text{ if } i \text{ is inserted at } x = 0. \tag{14}$$

Then, using (13) and (5) we find:

*Although an exact solution for the case of discrete individuals could have been obtained the continuous case was purposely chosen because it is simpler.

†δ_{ij} is the Kronecker delta: $\delta_{ij} = \begin{cases} 1 \text{ if } i = j \\ 0 \text{ if } i \neq j. \end{cases}$

$$\begin{aligned} f_{ij}(x+dx) &= \sum_{k=1}^{n} f_{ik}(x) Q_k(j)_{x,x+dx} \\ &= f_{ij}(x) - f_{ij}(x)\ \alpha n dx + \alpha dx\,. \end{aligned} \tag{15}$$

Thus $f_{ij}(x)$ satisfies the differential equation

$$f_{ij}'(x) + \alpha n f_{ij}(x) - \alpha = 0\,. \tag{16}$$

The solution, with the initial condition $f_{ij}(0) = \delta_{ij}$ is:

$$f_{ij}(x) = e^{-\alpha n x}\,\delta_{ij} + (1 - e^{-\alpha n x})/n\,. \tag{17}$$

IV. *Information Flow in the Game of Gossip.* According to (10), if $E(x)$ is the equivocation in the stretch of line $(0, x)$,

$$E(x) = -(1/n) \sum_{i,j=1}^{n} f_{ij}(x) \log f_{ij}(x)\,. \tag{18}$$

Substituting (17), manipulating algebraically, and inserting into (12) gives us as the basic result

$$\begin{aligned} R_n(x) = &\frac{1 + (n-1)e^{-\alpha n x}}{n} \log\left[1 + (n-1)e^{-\alpha n x}\right] \\ &+ \frac{(n-1)(1 - e^{-\alpha n x})}{n} \log(1 - e^{-\alpha n x})\,. \end{aligned} \tag{19}$$

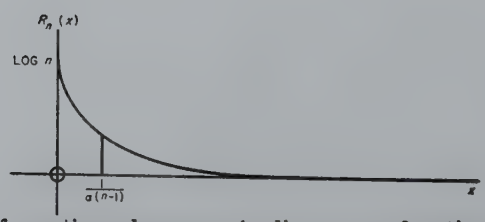

FIGURE 2. Information along gossip line as a function of distance from origin.

Here $R_n(x)$ is the information available at x regarding the original message. A plot of the function is given in Figure 2. As obvious checks we have

$$\lim_{X \to 0} R_n(x) = \log n\,, \tag{20}$$

$$\lim_{x \to \infty} R_n(x) = 0\,, \tag{21}$$

$$R_1(x) = 0\,, \tag{22}$$

$$\lim_{n\to\infty} R_n(x) = 0 \quad \text{when} \quad x \neq 0 . \tag{23}$$

It is interesting to evaluate the derivative of $R_n(x)$. This is

$$R_n'(x) = \alpha(n-1)\, e^{-\alpha n x} \log \left[\frac{1 - e^{-\alpha n x}}{1 + (n-1)\, e^{-\alpha n x}} \right] . \tag{24}$$

This shows that

(a) $R_n(x)$ is strictly decreasing as a function of x except when $\alpha(n-1) = 0$ in which case $R_n(x) \equiv$ const.

(b) The slope of $R_n(x)$ at the origin is infinite when $\alpha(n-1) \neq 0$.

V. *Estimates and Asymptotic Relations.* The following two relations are easily obtained from (19). For small x:

$$R_n(x) = \log n + \alpha(n-1)\, x \log x + 0\,(x^2 \log x). \tag{25}$$

For large n, and αx larger than some positive quantity independent of n:

$$R_n(x) = (3n/2)\, e^{-2\alpha n x} + 0\,(e^{-2\alpha n x}). \tag{26}$$

An interesting relation that can also be obtained is

$$\lim_{n\to\infty} \frac{R_n\left[\dfrac{1}{\alpha(n-1)}\right]}{R_n(0)} = 1/e \sim 0.37. \tag{27}$$

This indicates that for large n if we go out a distance $1/[\alpha(n-1)]$ from the origin we will find that the information has deteriorated to approximately 37% of its initial value.

VI. *Linear Electric Network Analogies.* Linear electric network analogy approximations can be obtained by exploiting either (26) or (27). Equation (25) cannot be used because the $x \log x$ term prevents it from being the solution of a linear differential equation with constant coefficients.

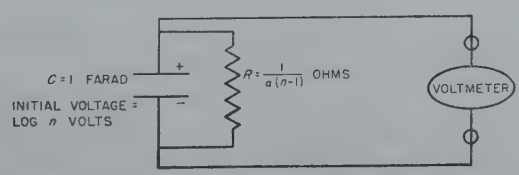

FIGURE 3. Approximate analogy for gossip line having frailty per unit distance α, for case of n possible messages. Here time is the quantity analogous to distance along the gossip line, and voltage is analogous to information.

An electric analogy could use either time or distance as the quantity analogous to x. If distance is used, we have the case of an electric transmission line with attenuation. Recognizing that a series combination of resistance R and capacitance C has a time constant RC seconds (time in which the original capacitor voltage goes to $1/e = 0.37$ of its initial value) a simple lumped analogy making use of (27) can be obtained. Namely, consider a capacitance of value 1 farad and leakage resistance $[1/\alpha(n-1)]$ ohms (Fig. 3). If the capacitance is originally charged to $\log n$ volts then the capacitor voltage as a function of time is approximately analogous to the information in the gossip line as a function of distance.

VII. *Supplementary Remark.* Of the several possible modifications of the preceding analysis that come to mind the most obvious one is the adoption of a different $Q_i(j)_{x,x+dx}$. This will simply change the differential equation (16), but the rest of the work would be the same. One possible example is to make α a function of x. This would reflect the effect of relative position in the group on the frailty of the individual.

LITERATURE

Brillouin, L. 1949. "Life, Thermodynamics, and Cybernetics." *Am. Sci.*, **37**, 554–68.

———. 1950. "Thermodynamics and Information Theory." *Ibid.*, **38**, 594–99.

Rashevsky, N. 1950. "Some Bio-Sociological Aspects of the Mathematical Theory of Communication." *Bull. Math. Biophysics*, **12**, 359–78.

Raymond, R. C. 1950. "Communication, Entropy, and Life." *Am. Sci.*, **38**, 273–78.

Reich, E. 1951. "Definition of Information." *Proc. Inst. Radio Eng.*, **39**, 290.

Rice, S. O. 1950. "Communication in the Presence of Noise." *Bell System Tech. Jour.*, **29**, 60–93.

Shannon, C. E. 1948a. "A Mathematical Theory of Communication." *Bell System Tech. Jour.*, **27**, 379–423.

———. 1948b. "A Mathematical Theory of Communication (Concluded)." *Ibid.*, **27**, 623–56.

———. 1949a. "Communication in the Presence of Noise." *Proc. Inst. Radio. Eng.*, **37**, 10–21.

———. 1949b. "Communication Theory of Secrecy Systems." *Bell System Tech. Jour.*, **28**, 656–715.

———. 1951. "Prediction and Entropy of Printed English." *Ibid.*, **30**, 50–64.

Wiener, N. 1948. *Cybernetics.* New York: John Wiley.

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A NOTE ON THE PROBLEM OF CYCLES IN RANDOM NETS

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The problem of cycles in random neural nets is considered. An approximation is derived giving the expected number $E(k, a, n)$ of cycles of length k of which a neuron in a random net will be a member.

The approximation is further simplified for the case $n >> k$. In this case $E(k, a, n) = a^k/n$, where (a) is the axone density of the net.

Consider a random net such as described by R. Solomonoff and A. Rapoport (1950). The "weak" connectivity of such a net is defined as the probability of the existence of a path through any number of internuncials between two arbitrarily chosen neurons N_1 and N_2.

The approximate method developed by Solomonoff and Rapoport gives the following equation for γ:

$$\gamma = 1 - e^{a\gamma}, \tag{1}$$

where (a) is the axone density of the net.

In particular, if N_1 and N_2 are identical γ gives the probability that there exists some path from N_1 back to N_1 through one or more internuncials. Therefore, γ is the probability that an arbitrary neuron of a random net is a member of a cycle.

For the case $a = 1$, a neuron can be a member of *at most* one cycle. For large n (the number of neurons in the net) the fraction of neurons that are members of cycles is vanishingly small, being proportional to $n^{-\frac{1}{2}}$.

For finite n and $a = 1$ the probability that a neuron is a member of a cycle of a *given size* has been given explicitly (see Rapoport, 1948, and Shimbel, 1948). Since in this case the probabilities that a neuron is a member of a cycle of m links and n links are mutually exclusive, it follows that γ is given by the sum of such probabilities.

However, for $a > 1$ a neuron can be a member of several *distinct* cycles, some of them possibly having neurons in common. Therefore, in this case γ cannot be derived as the sum of such mutually exclusive probabilities.

The problem can be approached in a slightly different way. Let $\phi_k^{(a)}$ be the probability that a randomly selected *path* of k links starting with a picked neuron of a set of n neurons each giving off (a) axones is a closed cycle.

By elementary considerations we find that

$$\phi_k^{(a)} = \frac{n-1}{n} \cdot \frac{n-2}{n} \cdots \frac{n-k+1}{n} \cdot \frac{1}{n}. \tag{2}$$

From expression (2) we obtain the relation

$$\phi_k^{(a)} = \frac{n!}{n^{k+1}(n-k)!}. \tag{3}$$

Using Stirling's formula on equation (3) we obtain

$$\phi_k^{(a)} = \frac{n^{n+\frac{1}{2}}}{n^{k+1}(n-k)^{n+\frac{1}{2}} e^k}. \tag{4}$$

Now if we multiply $\phi_k^{(a)}$ by the total number of paths T of k links which can be taken starting with a given neuron we obtain an approximation to the expected number $E(k, a, n)$ of cycles of length k which a randomly selected neuron will be a member of. Thus we have

$$E(k, a, n) = \phi_k^{(a)} T. \tag{5}$$

Moreover the total number of possible paths of k links starting with a given neuron is equal to a^k. We obtain this expression by considering that the "first step" of the path can be taken along any one of (a) axones. The second step can also be made in (a) different ways so that a path of k links can be made in $a \cdot a \cdot a \cdot a \cdots$ (k times) different ways.

From this we find that

$$E(k, a, n) \approx \frac{n^{n-k-\frac{1}{2}}}{(n-k)^{n+\frac{1}{2}}} \left(\frac{a}{e} \right)^k. \tag{6}$$

Expression (6) is only an approximation because the paths of k links which can be taken starting from a given neuron *are not* entirely independent. Any two paths in the a^k different possible ones may have one or more links in common. Also two effectively identical cycles (in terms of neurons) may differ in that distinct axone paths may exist. For these reasons expression (6) does not strictly follow the definition of expected number.

For the cases $k = 2$, $a = 1$ and $k = 2$, $a = 2$ the expression

$\phi_k^{(a)} a^k$ accurately gives the expected number as tested from an exact formulation. The accuracy of expression (6) for increasing k and a is yet to be determined.

Note that for $n >> k$, $\phi_k^{(a)}$ is very close to $1/n$. This means that for $n >> k$ we can write

$$E(k, a, n) = \frac{a^k}{n}. \tag{7}$$

In view of the extreme complexity implied by the exact formulation, expression (7) seems suprisingly simple. Each of the pertinent variables appears only once in the function.

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LITERATURE

Rapoport, A. 1948. "Cycle Distributions in Random Nets." *Bull. Math. Biophysics*, **10**, 145–57.

Shimbel, A. 1948. "An Analysis of Theoretical Systems of Differentiating Nervous Tissue." *Bull. Math. Biophysics*, **10**, 131–43.

Solomonoff, R., and A. Rapoport. 1950. "Connectivity of Random Nets." *Bull. Math. Biophysics*, **13**, 107–17.

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A NEUROBIOPHYSICAL INTERPRETATION OF CERTAIN ASPECTS OF THE PROBLEM OF RISKS

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A situation is considered in which an individual is given an opportunity to risk a certain amount of money or goods in order to gain a larger amount, providing the result of some uncertain event proves favorable. A neural mechanism is introduced in which the probability of success can be ordered according to its value. The response to a situation thus becomes dependent upon the probability. An expression is then derived for the amount that would be risked in terms of the probability and of the amount that would be gained in the event of a successful outcome. Similar expressions are obtained for the case of insurance against loss. Results of questionnaires indicate that individuals can be classified according to their pattern of behavior in the situation considered. The various types can be most easily recognized when a plot is made of the relative amount risked against the probability of success. In a general way, these types can be understood in terms of the equations derived.

The situation which we shall consider is one in which an individual is given an opportunity to risk a certain amount f of goods for the chance to obtain an amount v, under circumstances in which the probability of success is α. Our problem is to derive a function $f(v, w, \alpha)$, w being a measure of the quantity of goods possessed by the individual.* In order to do this we must first treat certain component parts of the problem. Therefore, we shall discuss a mechanism by which the fraction of successes, in a given situation, is abstracted. Thus to a given process, which on repeated observation is found to have a certain fraction of successful outcomes, there is a corresponding neural element [at $\bar{x}(\alpha)$]; and the correspondence depends only on the value of the fraction (α). Another mechanism is then introduced which makes it possible for the effective value of the stimulus (v) to be reduced by any given fraction (α'), the value depending upon which one of a series of neural elements $N_{\alpha'}$ is acting at the same time as the stimulus. Through a process of conditioning, the

*A better approximation might be a linear combination of the amount possessed, the rate of income, and the rate of outflow of goods.

elements corresponding to probabilities [at $\bar{x}(a)$] become functionally connected to the elements ($N_{a'}$) which affect the response to the stimulus (v). The result is that the effective value of the stimulus depends upon both the stimulus magnitude (v) and its associated probability (a). The problem, then, is reduced to that of a choice between two alternatives: taking or not taking the risk. To each alternative there corresponds a net effective stimulus value. The risk is taken if the stimulus value for this situation is the larger one.

Mechanism for the Representation and Ordering of Probabilities. Consider a test situation which can only result in a successful or unsuccessful outcome. Suppose that this situation has been observed by an individual to give αn successes out of n trials. Let a group of neurons M_i represent the memory traces from each one of the observed trials. Let each of these neurons M_i act upon the two neurons M' and M'' (Fig. 1). For convenience, the neurons M_i are grouped in Figure 1 in such a manner that the αn corresponding to the successful outcomes are together. Due to conditioning the M_i corresponding to successful events will have greater effects upon M' and M'' than those corresponding to unsuccessful trials. In Figure 1 this difference is indicated by the use of two end bulbs and one end bulb, respectively. Let the thresholds of M' and M'' be one and two, respectively. Let ν_{M_i} be the average frequency of firing of M_i. If the ν's

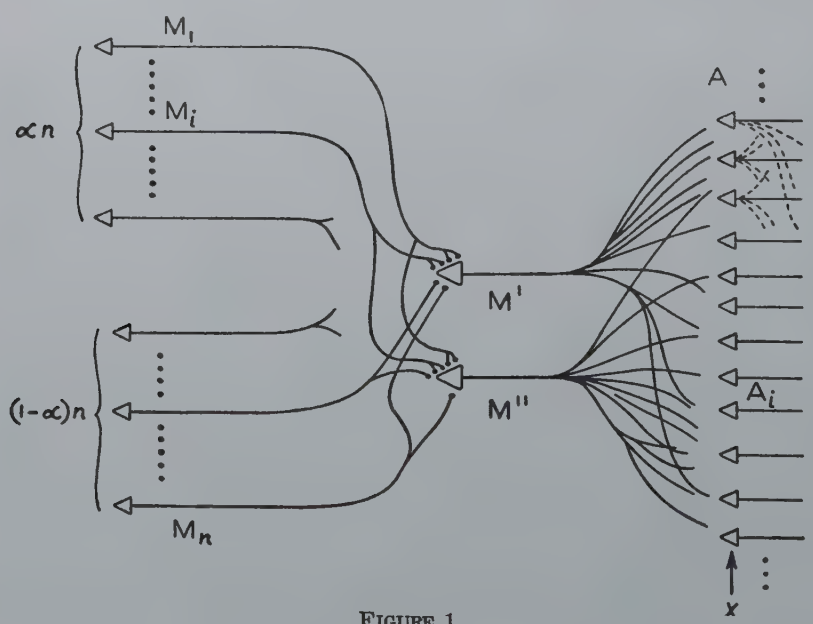

FIGURE 1

are, on the average, equal to $\bar{\nu}$, then the average frequency of action of M' and M'' will be

$$\nu_{M'} = \nu_{M_1} + \cdots + \nu_{M_i} + \cdots \nu_{M_n} = \bar{\nu} n; \tag{1}$$

$$\nu_{M''} = \nu_{M_1} + \cdots \nu_{M_{\alpha n}} = \bar{\nu} \alpha n. \tag{2}$$

Let M' and M'' send collaterals to each element in the center A, each sending different numbers in different parts of A. The neurons in A are arranged linearly so that we may refer to the neurons at a position x. Furthermore, we consider the number of collaterals reaching A to be sufficiently large so that we may define a density of the endings at x. Let the density at x of those originating at M' and M'' be $E_{\alpha n}(x)$ and $E_n(x)$, respectively. Then the total excitation at x is given by $\alpha n E_{\alpha n}(x) + n E_n(x)$. In general, the total excitation depends upon x and upon α. If there is a point $\bar{x}$ at which the total excitation is a maximum, this can be found by differentiating the above expression and setting the derivative equal to zero. If this is done and the resulting expression is solved for α, we find $(E' = dE/dx)$:

$$\alpha(\bar{x}) = -E_n'(\bar{x})/E_{\alpha n}'(\bar{x}). \tag{3}$$

In the following we shall assume that the resulting relationship $\alpha(\bar{x})$ is monotonic, although it is probably necessary only that $\bar{x}(\alpha)$ be single-valued. The elements of A are considered to mutually inhibit each other in such a manner that only those elements in the neighborhood of $\bar{x}$ are able to transmit (cf. Rashevsky, 1948, p. 377).

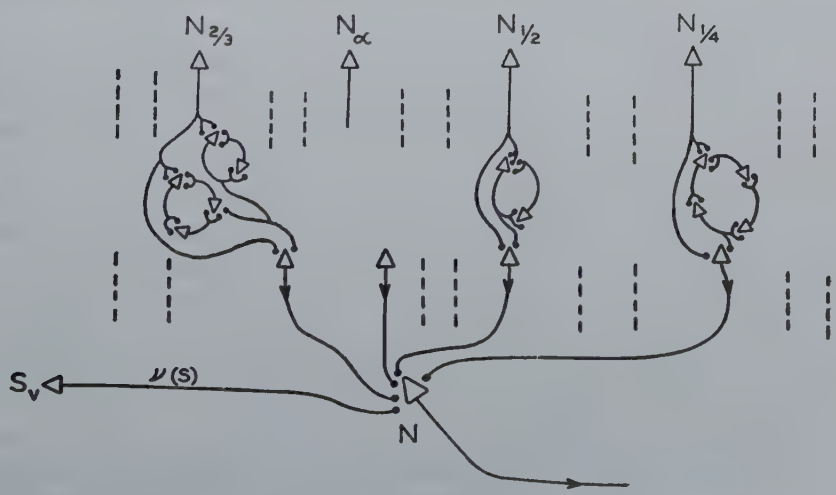

FIGURE 2

A Mechanism for Altering an Input Frequency by Various Fractions. Let a stimulus of intensity S_v (Fig. 2) result in a frequency ν of impulses, the frequency depending upon the intensity. If during the same period of time a neuron N_α is firing at a frequency $1/\delta$, δ being the absolute refractory period, then neuron N (Fig. 1), with a threshold of 2, fires with an average frequency

$$\nu_N = \alpha\nu(S_v). \tag{4}$$

This follows since the fraction of time that N_α sends impulses to N is, by construction, equal to α. The thresholds are taken to be equal to two unless indicated to the contrary. The assumption that the N_α fire with frequency $1/\delta$ is not as restrictive as it might first appear. Although each N_α results in a periodic pattern of impulses, the effect is to reduce $\nu(S_v)$ by a fraction α on the average only, since, in general, S_v results in a random temporal sequence.

It is essential that only one N_α act at a given time. In order to insure this the N_α must mutually inhibit one another (not shown in Fig. 1) in such a manner that only one element is able to transmit, even if several neighboring elements should be stimulated simultaneously.

The net of Figure 2 gives a spatial correspondence $\bar{x}$ in A to the fraction α of successful events. We will now suppose that there are non-functioning connections between each element in A of Figure 2 and each element S_α of Figure 1. Let these connections be of such a kind that they can become functional through conditioning. Consider, for a moment, two stimuli S_1 and S_2 which represent situations with probabilities of successes α_1 and α_2. In a situation in which there is a choice between these two, the best result, on the average, occurs when the stimuli are weighted by their respective probabilities. Thus when S_1 is, by chance, weighted by an amount α_1, due to the simultaneous action of S_1 and S_{α_1}, the result is likely to be more favorable than when S_1 and some other S_α act together. But when S_1 is brought into activity, the neurons in the region about $x(\alpha_1)$ become active because of the mechanism of Figure 2. Therefore the degree of conditioning between $\bar{x}(\alpha_1)$ and S_{α_1} tends to be greater than that between $\bar{x}(\alpha_1)$ and any other S_α. Under these conditions, then, a stimulus S, whose probability of success is α, tends to result in an output frequency of value $\alpha\nu(S)$ instead of $\nu(S)$.

In the above argument we have assumed that the failures produce no extinction in the conditioning process. If we did not assume this, the more uncertain event would be given less weight than its

corresponding value α. A more detailed analysis would be required to evaluate this effect.

The Determination of the Function f(v, w, α): *Risk for Gain.* We return now to the situation originally proposed. We shall use an expression of the following form for the relation $\nu(S_v)$:

$$\nu(S_v) = A \log(1 + \gamma S_v). \tag{5}$$

This type of relation has been commonly used in mathematical investigations of the central nervous system and of social behavior (Rashevsky, 1948, 1950). The number 1 is used in the argument of the logarithm to avoid introducing discontinuities and threshold phenomena.

We shall suppose in the choice between two alternatives that one is chosen because of the greater net excitation at some level C. If the situation presents a choice of taking or not taking a risk for some gain, then, according to our model, we need only compare the net excitations corresponding to the two situations to determine the outcome (Landahl, 1938). In so doing we neglect any random phenomena which would lead to distributions of the probabilities of the amounts that would be risked under given circumstances.

In the situation under consideration, failure to take the risk would result in the individual's possessing exactly what he already had, that is, w. As the only stimulus is $S_v = w$, in this case we would have the following excitation at C:

$$A \log(1 + \gamma w) = A\alpha \log(1 + \gamma w) + A(1 - \alpha) \log(1 + \gamma w).$$

If the risk is taken and the result successful, an excitation corresponding to this would be given by equation (4). In (4) α has the same meaning as here and $\nu(S_v)$ is given by equation (5), with $S_v = w + v - f$, $v - f$ being the gain. In the event of failure, the excitation would be given by equations (4) and (5) with α replaced by $(1 - \alpha)$, the probability of failure, and $S_v = w - f$, f being the loss. The total excitation due to these two possibilities is then:

$$A\alpha \log(1 + \gamma w + \gamma v - \gamma f) + A(1 - \alpha) \log(1 + \gamma w - \gamma f).$$

If no other factors are taken into account, then f, the maximum value that would be offered, is given by equating the degrees of excitation corresponding to these situations. From this we obtain:

$$A\,\alpha \log\left(\frac{1 + \gamma w + \gamma v - \gamma f}{1 + \gamma w}\right) + A(1 - \alpha) \log\left(\frac{1 + \gamma w - \gamma f}{1 + \gamma w}\right) = 0, \tag{6}$$

from which we can calculate f in terms of v, w, and α.

From our previous discussion it is clear that the weighting by α and $(1-\alpha)$ is only to be expected in the absence of any extinction. The more general case can be included if the two coefficients A in (6) are made functions of α and $(1-\alpha)$ respectively. Since a generally is small, we may introduce A for the first and $A(1+\beta)$ for the second to allow, to some extent, for this effect. This could be interpreted as meaning that the anticipated gain and loss are not equally weighted.

In addition to this effect we shall consider the effect of the prize, and the excitation or inhibition due to the situation. When α is equal to zero or one, there is no uncertainty. Thus an expression of the form

$$Aa_0(a^{\varepsilon}-a)\log\left(1+\frac{v}{w}\right)\equiv Aa\log\left(1+\frac{v}{w}\right) \tag{7}$$

may be used for the stimulus value of the prize. The quantities $a_0 \geq 0$ and ε are constants and a is defined by expression (7).

For the contribution due to the individual's attitude toward situation we shall add a quantity of the form

$$Ab = Ab_0(a^{\varepsilon'}-\alpha), \tag{8}$$

where b may be either positive or negative, depending upon whether the situation is interpreted as pleasant or unpleasant.

If we add either terms of (7) or (8) to expression (6), and make the generalization indicated above, we obtain the expression:

$$\begin{aligned}\alpha\log\frac{1+\gamma w+\gamma v-\gamma f}{1+\gamma w}+(1+\beta)(1-\alpha)\log\frac{1+\gamma w-\gamma f}{1+\gamma w}\\ +a\log\left(1+\frac{v}{w}\right)+b=0,\end{aligned} \tag{9}$$

from which we can obtain $f(v, w, \alpha)$.

From equation (8) we can see that if $\alpha=0$, $f=0$, and $a=1$, then $f=v$. Now suppose that $a=a_0$ and $b=b_0$, except for $\alpha=0$ and 1, and let $w >> 1/\gamma$, $v << w$ and $a << 1$. We shall define

$$R=\frac{f}{\alpha v}. \tag{10}$$

Then, expanding (9), we have (after rearrangement):

$$R=\frac{1+a/\alpha+bw/\alpha v}{1+\beta-\alpha\beta}-\frac{v(a^2+\alpha\beta+\alpha^2\beta+\alpha-\alpha^2)}{2w\alpha(1+\beta-\alpha\beta)^2}+\cdots. \tag{11}$$

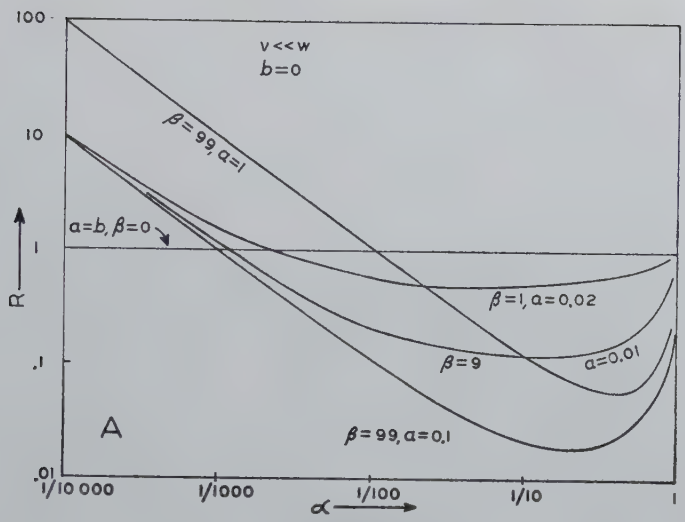

FIGURE 3*a*

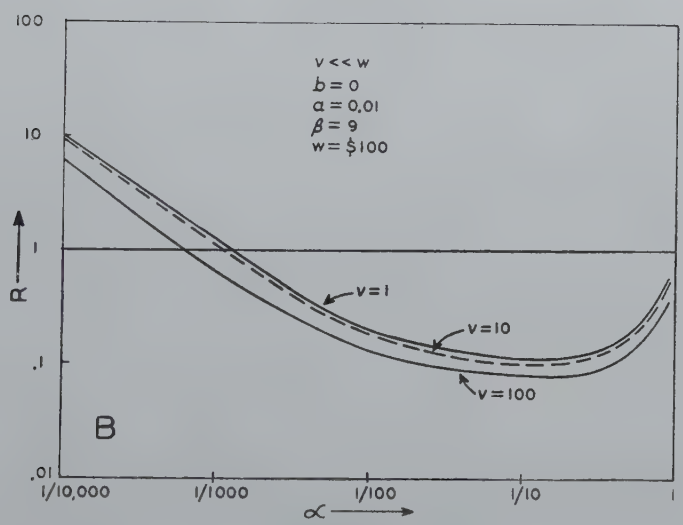

FIGURE 3*b*

In Figure 3 some examples of the types of relations which may occur for selected values of the parameters are graphically shown. Except for the case of Figure 3b, the results are obtained from the simplified expression (11). From these graphs it can be seen that, depending upon the choice of parameters, rather different types of curves can be obtained.

In order to ascertain what types of relations might actually oc-

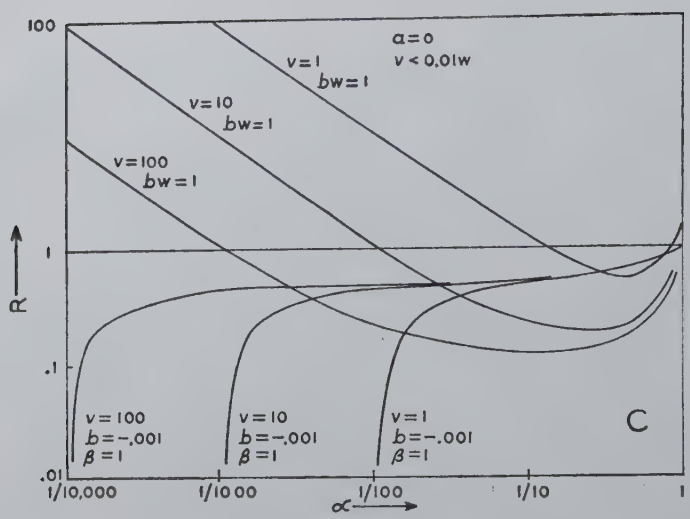

FIGURE 3c

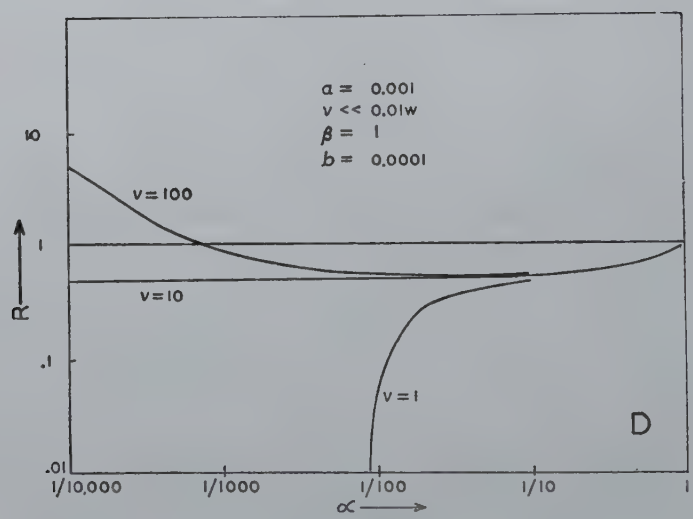

FIGURE 3d

cur, a number of subjects were given an opportunity to offer various amounts for various prizes ($1, $10, $100), in situations in which the probabilities (10^{-4} to 3/4) were stated. The subject was given a statement of the prize v and probability α for each situation; then a restatement in different terms. For example: "Prize—$10, chances 1 in 10; if each of ten individuals contributes $1 to a total prize of $10, the most I would pay for a chance to win is ———." Then followed a set of

values. The subject was instructed to proceed from the low values until he reached the last value he would offer for a chance at the prize. This value was recorded by the subject to avoid possible psychological pressure on him by the experimenter. Most subjects were told that the experimenter reserved the right, within the day, to expect the subject to accept an offer for any one of the situations at the price recorded by the subject. For 26 subjects (18 male, 8 female) the set of questions was given three times, usually on different days. For some individuals the results were very uniform; for others the results were highly erratic. For this reason the result of averaging was occasionally ambiguous. Wherever the mean was close to the median, the former was used; otherwise, the mean and median were averaged. If the subject was unwilling to offer one cent, he was given an opportunity to give the number of chances for which he would pay one cent.

The results from these subjects indicated that there are perhaps four primary types of curves. In one group the relation between R and α is one in which there is a continuous decrease in R with α up to a value of 3/4. The slopes and the positions of the curves vary from individual to individual. Six of the twenty-five subjects were in this group. An example is shown in Figure 4b. In some cases two of the curves (e.g., $v = \$1$ and $v = \$10$) would almost overlap.

A more or less pronounced minimum in the curves appeared in a second group. It was less pronounced and often absent for $v = 1$. Figure 4a shows an example of this group. In several cases the mini-

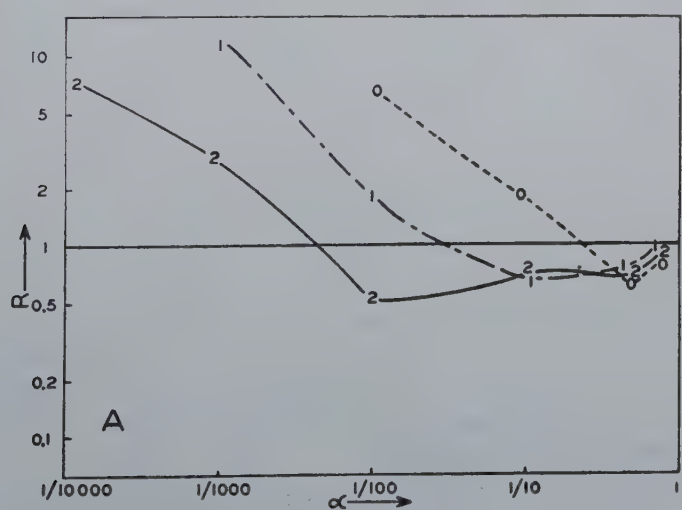

FIGURE 4a

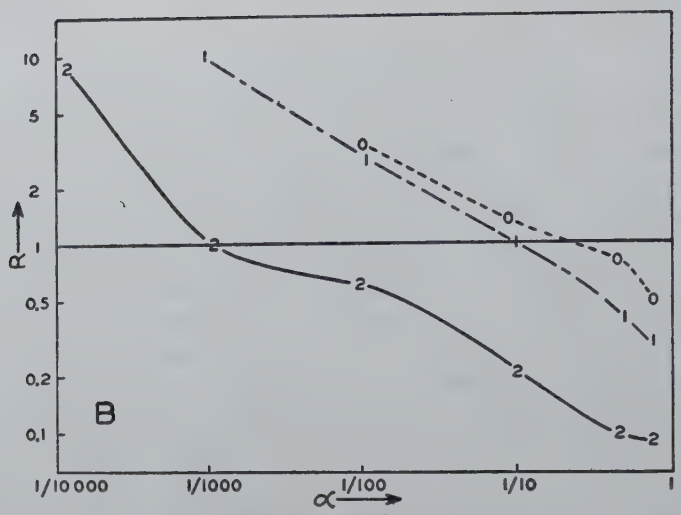

FIGURE 4b

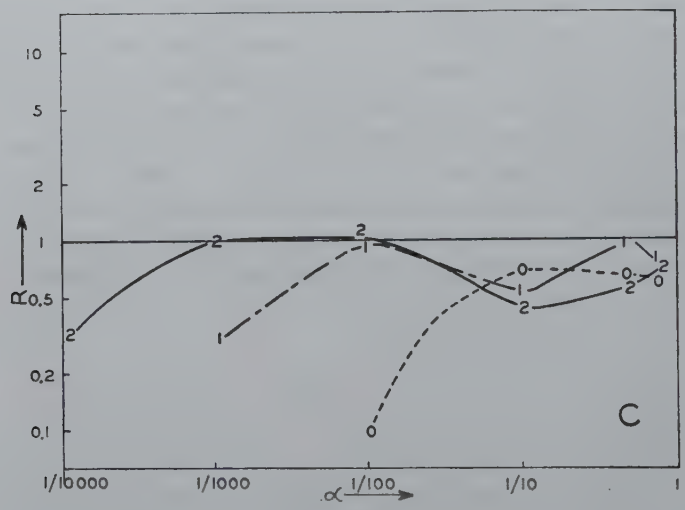

FIGURE 4c

mum is much more pronounced than in the example shown. In general, the order in which the curves occur is the same as in Figure 4b, although, for example, the curves for $v = 1$ and $v = 10$ would overlap or even invert for one individual. The curves for $v = 1$ and $v = 100$, however, were never inverted. Out of the twenty-five cases, seven would best fall into this class.

Since the values of α close to unity were not used, it is not possible to determine whether or not the above groups differ only in the

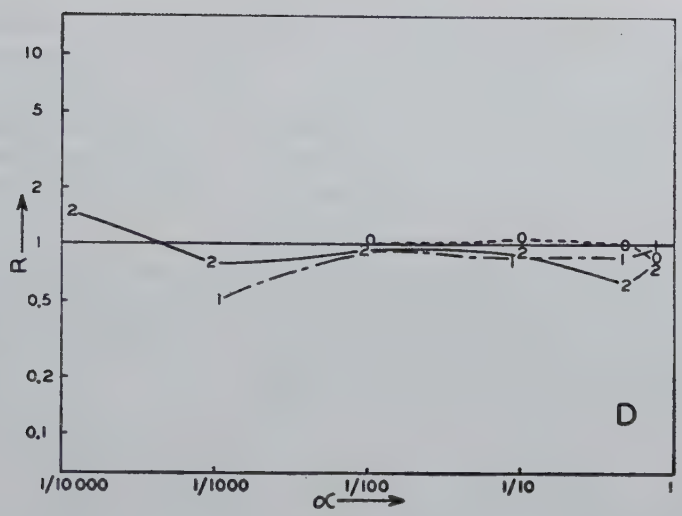

FIGURE 4*d*

position of the minimum. Furthermore, irregularities in the curves often make the existence of a minimum uncertain. Thus six subjects could be equally well classified into group one or two.

A third group, in which there were four cases, is illustrated by the example in Figure 4c. The feature characterizing this group is the decrease in R with decreasing α. In one case the curves for $v = 1$, $v = 10$, and $v = 100$ were practically superimposed.

Two other subjects could be characterized by their R values being roughly constant. One was very erratic, the other quite regular. The results for the latter individual are shown in Figure 4d. It may be that this case is more similar to the case shown in Figure 3d.

There was no evidence to suggest a sex difference in the type of response.

Since there are such great differences in the responses in the different groups, averaging, depending on the method used, gives very different results. An arithmetic average results in a curve for the ratio R which is greater than unity for small values of α and smaller than unity for values of α greater than about 10^{-1} (Preston and Baratta, 1948).

Of eighteen other individuals who were given the questionnaire only once, three made no offers, four made offers very much smaller than any in the above groups, and three could be fairly satisfactorily classified into group one, seven into group two, one into the fourth group and one resembled Figure 3d.

No offers were actually made to any subject at the time the questionnaires were distributed. However, each of seven of the subjects was offered a chance at the median value of his own offers for a selected value of α and v. Value of α from 1/100 to 1/2 and values of v of \$1 and \$10 were used. The offers were accepted in all seven cases. The subjects on the whole were neither anxious to accept nor reject the offers .

The Determination of $g(L, w, \alpha)$: *Insurance against Loss.* We may next ask what amount g would be given in exchange for security against a loss L. If the amount g is given out, the result will be

$$A \log(1 + \gamma w - \gamma g) = A\,\alpha \log(1 + \gamma w - \gamma g) + A(1 - \gamma)\log(1 + \gamma w - \gamma g).$$

Otherwise, if α is now the probability of loss, it would be

$$A\,\alpha \log(1 + \gamma w - \gamma L) + A(1 - \alpha)\log(1 + \gamma w).$$

The prospect of loss may also act as an unpleasant stimulus. If we consider that its effect is just the same as a negative prize, then, the effect would be the same, except that v is replaced by $-L$. In the previous case the prize could be anticipated in the immediate future, while in this case the loss may occur in the distant future at an uncertain time. For this reason a and b are primed. Thus we have the following expression from which to determine $g(L, w, \alpha)$:

$$\alpha \log \frac{1 + \gamma w - \gamma g}{1 + \gamma w - \gamma L} + (1 + \beta')(1 - \alpha)\log \frac{1 + \gamma w - \gamma g}{1 + \gamma w} - a' \log(1 - L/w) - b' = 0. \tag{12}$$

The β' is introduced somewhat arbitrarily, as in (6). Since α has a different meaning here, and since the time of occurrence of the loss is uncertain in this case, β may be quite different; hence it is primed. As in the previous case, a more detailed study is required to evaluate β'.

If $\alpha = 0$, then, from (11), $g = 0$. If $\alpha = 1$, then $g = L$. For $\gamma w >> 1$, $a << 1$, $L << w$, we find approximately the same expression for $g/\alpha L$ as for $f/\alpha v$ of (11); however v is replaced my minus L. This makes $g/\alpha L$ greater than unity for large L/w and for small α. Unless L/w is small, α is not too small, and β' is small, g/L will exceed α. The conditions for which $g/\alpha L$ will exceed unity are, therefore, more likely to be met in this case than in the previous case of $f/\alpha v$.

It would be of interest to relate the parameters in equation (12) with those of equation (9). A more detailed study would first be required to elaborate upon the quantities which have been replaced by the parameters β and β'. One then might be in a position to predict correlations between the parameters.

LITERATURE

Landahl, H. D. 1938. "Contribution to the Mathematical Biophysics of Psychophysical Discrimination." *Psychometrika*, **3**, 107–25.

Preston, M. G. and P. Baratta. 1948. "An Experimental Study of the Auction Value of an Uncertain Outcome." *Am. Jour. Psychol.*, **61**, 183–93.

Rashevsky, N. 1948. *Mathematical Biophysics*. Rev. Ed. Chicago: University of Chicago Press.

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BOOK REVIEW

JAMES T. CULBERTSON. *Consciousness and Behavior: A Neural Analysis of Behavior and Consciousness.* 1950. 210 pp. Dubuque, Ia.: Wm. C. Brown Co. $4.25.

Whether or not the so-called "digital" approach to the central nervous system will become a well-beaten path in theoretical physiology will be determined among other things by the exploration of its implications. This job is undertaken with remarkable thoroughness by James T. Culbertson of the School of Philosophy at the University of Southern California in his book *Consciousness and Behavior.*

The digital model of the central nervous system was first rigorously described in this journal by W. S. McCulloch and W. Pitts (*Bull. Math. Biophysics,* 5, 115-33) and has undergone considerable theoretical development by N. Rashevsky, H. D. Landahl, J. Roberts, and others.

By theoretical development of a model we mean an investigation of what the model can do. Part one of Dr. Culbertson's volume is devoted to such an investigation. He shows, for example, the construction of digital type neural nets which give invariant responses to "cardinal number," i.e., responses where the stimulation of a certain number of elements results in a firing of a particular neuron, regardless of *which* elements were stimulated. Next the "bottle neck" problem is solved in terms of the digital net. It is shown how one-to-one mapping from one set of neurons to another can be accomplished even though the number of connecting fibers between the sets is smaller than the number of neurons to be mapped. General questions concerning the transmission of "information" in digital nets are raised in relation to this specific problem, which originally came to the attention of neuro-physiologists in connection with the mapping of the visual retina upon the striate area.

Further, Dr. Culbertson treats the problem of *gestalt* in connection with the recognition of contour shapes and proposes a model somewhat similar to but not identical with that of Pitts and McCulloch (*Bull. Math. Biophysics,* 9, 127-47). It is also considerably more specific and detailed than the Pitts-McCulloch model.

Finally the problem of long-term detailed memory is treated on the basis of "synaptic variation," a formal postulate implying that end bulbs, previously ineffective in eliciting the firing of the neuron on which they synapse, become effective if, when they are active, the neuron is fired by other effective bulbs. This postulate has also been proposed by D. O. Hebb (*Organization of Behavior*), by A. Shimbel (*Bull. Math. Biophysics,* 12, 241–75), and by others. The advantage of this hypothesis is that it obviates the necessity of explaining learning and conditioning processes in terms of reverberating circuits and thus is "neuro-economical," to use Dr. Culbertson's term. The synaptic variation hypothesis also seems more reasonable to some authors (e.g., Hebb) in accounting for long range learning and memory processes than reverberating circuits, which are believed to be active only for short periods of time. The formal implications of the sypnatic variation hypothesis are, however, entirely analogous to those derived from reverberating circuits in the conditioning process.

Part two of *Consciousness and Behavior* is devoted to a theory of consciousness and sensation, which Dr. Culbertson prefers to treat separately from the theory of behavior. The philosophical reasons for this Cartesian dichotomy are stated by the author in a futuristic skit in which Troglodyte Titchno, a leader of a small rebellious band of "neo-structuralists," shouts defiance at his captors,

apparently the entrenched intellectual rulers of 2000 A.D., who have succeeded in banning all considerations of consciousness from Official Psychology.

The polemic is spirited, and the theory of psycho-spaces proposed by Dr. Culbertson in his support of the neo-structuralist thesis is original and provocative but entirely beyond the scope of this journal.

Some quaint effects result from Dr. Culbertson's use of integers instead of algebraic symbols to designate numbers of neurons involved. Thus we read expressions like this: "If 264 cells fire in P and 746 cells fire in Q . . . . ." This usage is, however, in harmony with Dr. Culbertson's extremely explicit treatment of his models. In this reviewer's opinion, this minor eccentricity adds to rather than detracts from the general clarity of treatment and the unique charm of Dr. Culbertson's style, which sets this book apart among philosophical dissertations.

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INDEX TO VOLUME 13

INDEX OF AUTHORS

PAGE

ACKERMAN, EUGENE. Resonances of Biological Cells at Audible Frequencies 93

ANDERSON, NORMAN AND ANATOL RAPOPORT. A Note on Facilitation and Threshold Phenomena 47

EPSTEIN, HERMAN T. AND ANATOL RAPOPORT. A Note on the McCulloch-Pitts Neural Net for Heat-Cold Discrimination 21

GEMMILL, C. L. AND R. L. PLUNKETT. The Kinetics of Invertase Action 303

HEARON, JOHN Z. A Note on the Equations of Conditioned Reflex 23

KARREMAN, GEORGE. Contributions to the Mathematical Biology of Excitation with Particular Emphasis on Changes in Membrane Permeability and on Threshold Phenomena 189

LANDAHL, H. D. A Neurobiophysical Interpretation of Certain Aspects of the Problem of Risks 323

LANDAU, H. G. On Dominance Relations and the Structure of Animal Societies: I. Effect of Inherent Characteristics 1

LANDAU, H. G. On Dominance Relations and the Structure of Animal Societies: II. Some Effects of Possible Social Factors 245

LANDAU, H. G. AND A. T. REID. A Suggested Chain Process for Radiation Damage 153

LEVINSOHN, S. A Note on Rapoport's Approximate Formula for the Input-Output Curve in the Case of Bilateral Pre-Inhibition 39

MCGILL, WILLIAM J. AND WALTER A. ROSENBLITH. Electrical Responses to Two Clicks: A Simple Statistical Interpretation 69

OPATOWSKI, I. On Permeability Determination of the Erythrocyte 27

OPATOWSKI, I. On the Mathematical Theories of Excitation . . 41

PAGE

OPATOWSKI, I. On Simultaneous Determinations on the Permeability of a Membrane and of the Diffusion Coefficient in an Adjacent Medium 119

OPATOWSKI, I. Determination of the Sensitive Volume by Irradiation and the Ionization Density 263

OPATOWSKI, I. AND F. R. TANGHERLINI. Diffusion and Recombination of Products of Ionizing Radiations 273

PLUNKETT, R. L. AND C. L. GEMMILL. The Kinetics of Invertase Action 303

RAPOPORT, ANATOL. Nets with Distance Bias 95

RAPOPORT, ANATOL. The Probability Distribution of Distinct Hits on Closely Packed Targets 133

RAPOPORT, ANATOL. "Addition" and "Multiplication" Theorems for the Inputs of Two Neurons Converging on a Third . 179

RAPOPORT, ANATOL AND NORMAN ANDERSON. A Note on Facilitation and Threshold Phenomena 47

RAPOPORT, ANATOL AND HERMAN T. EPSTEIN. A Note on the McCulloch-Pitts Neural Net for Heat-Cold Discrimination . 21

RAPOPORT, ANATOL AND RAY SOLOMONOFF. Connectivity of Random Nets 107

RASHEVSKY, N. Suggestions for a Mathematical Biology of Some Cultural Developments 51

RASHEVSKY, N. Outline of a Mathematical Biosociology of Beliefs and Prejudices 61

RASHEVSKY, N. A Suggestion for a Mathematical Approach to the Problem of the Effect of Climatic Factors on Health 79

RASHEVSKY, N. A Note on the Theory of Communication through Social Channels 139

RASHEVSKY, N. A Note on Imitative Behavior and Information 147

RASHEVSKY, N. Mathematical Biosociology of Beliefs and Prejudices 289

REICH, EDGAR. The Game of "Gossip" Analyzed by the Theory of Information 313

PAGE

REID, A. T. On the Diffusion of Metabolic Intermediates . . . 31

REID, A. T. AND H. G. LANDAU. A Suggested Chain Process for Radiation Damage 153

ROSENBLITH, WALTER A. AND WILLIAM J. MCGILL. Electrical Responses to Two Clicks: A Simple Statistical Interpretation 69

SHIMBEL, ALFONSO. Applications of Matrix Algebra to Communication Nets 165

SHIMBEL, ALFONSO. A Note on the Problem of Cycles in Random Nets 319

SOLOMONOFF, RAY AND ANATOL RAPOPORT. Connectivity of Random Nets 107

TANGHERLINI, F. R. AND I. OPATOWSKI. Diffusion and Recombination of Products of Ionizing Radiations 273

INDEX OF SUBJECTS

Animal societies, structure of, 1, 245

Beliefs and prejudices, 61, 289
Bilateral pre-inhibition, 39
Biological cells, resonances of at audible frequencies, 93

Climatic factors, effect of on health, 79
Communication
  nets, 165
  theory of, 139
Conditioned reflex, equations of, 23
Cultural developments, 51
Cycles in random nets, 319

Diffusion coefficient, determination of, 119
Diffusion
  and recombination, 273
  of metabolic intermediates, 31
Dominance relations, 1, 245

Electrical responses to two clicks, 69
Erythrocyte, permeability determination of the, 27
Excitation
  mathematical biology of, 189
  mathematical theories of, 41

Facilitation and threshold phenomena, 47

"Gossip," game of, 313

Health, effect of climatic factors on, 79
Heat-cold discrimination, 21
Hits on closely packed targets, 133

Information, 147
  theory of, 313
Imitative behavior, 147
Invertase action, kinetics of, 303
Ionization density, 263
Ionizing radiation, 273
Irradiation, 263

Kinetics of invertase action, 303

McCulloch-Pitts neural net, 21
Membrane permeability, 189

Membrane, permeability of a, 119
Metabolic intermediates, 31

Nets
communication, 165
with distance bias, 85
Neurons, inputs of two converging on a third, 179

Permeability determination of the erythrocyte, 27

Radiation damage, chain process for, 153
Random nets
connectivity of, 107
cycles in, 319
Risks, problem of, 323

Sensitive volume, determination of, 263
Social channels, communication through, 139

Theory
of communication, 139
of information, 313
Threshold phenomena, 47, 189

BOOK REVIEW

JAMES T. CULBERTSON, Consciousness and Behavior: A Neural Analysis of Behavior and Consciousness (Reviewed by Anatol Rapoport) - - - 337